Pawnee montane skipper *Hesperia leonardus montana* Skinner (Lepidoptera: Hesperiidae): Habitat Requirements, Distribution and Abundance, Population Responses to Forest Thinning and Wildfire, and Genetic Investigations

Lepidoptera of North America 19

Contributions of the C.P. Gillette Museum of Arthropod Diversity, Department of Agricultural Sciences, Colorado State University

Cover Images:

Clockwise from top: *Hesperia leonardus montana* male nectaring on *Symphyotrichum laeve*; *Hlm* female ovipositing on *Bouteloua gracilis*; *Hlm* female nectaring on *Liatris punctata*. All photos taken near Deckers CO by Boyce Drummond (Research Associate, C.P. Gillette Museum of Arthropod Diversity)

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Pawnee Montane Skipper *Hesperia leonardus montana* Skinner (Lepidoptera: Hesperiidae): Habitat Requirements, Distribution and Abundance, Population Responses to Forest Thinning and Wildfire, and Genetic Investigations

By:

Scott Ellis

2055 Bonner Springs Ranch Road

Laporte, Colorado 80535

e-mail: oeneis@gmail.com

John Sovell

Colorado Natural Heritage

Colorado State University

Fort Collins, Colorado 80525

e-mail: johnsovell@colostate.edu

Mikele Painter

Pike National Forest

South Platte Ranger District

Conifer, Colorado 80433

e-mail: mikele.painter@usda.gov

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Contributions of the C.P. Gillette Museum of Arthropod Diversity, Department of Agricultural Sciences, Colorado State University

Table of Contents

Abstract

This Contribution summarizes field studies conducted between 1985 and 2021 on the habitat and biology of the federally listed Pawnee montane skipper butterfly (*Hesperia leonardus montana* Skinner) and its population responses to forest thinning treatments and large wildfires within the same time frame. Other smaller studies and genetic information are also summarized.

H. l. montana (Hlm) occupies a total known range of less than 80 square miles within the South Platte River drainage southwest of Denver, Colorado. Habitat consists of xeric conifer woodland dominated by an overstory of ponderosa pine (*Pinus ponderosa*), an understory of blue grama grass (*Bouteloua gracilis*), which is the larval foodplant, and dotted gayfeather (*Liatris punctata*), the primary adult nectar source. Peak adult Hlm densities during late August to early September generally ranged from 1 to 4 individuals per acre.

Based on Hlm densities measured in 1986 belt transects, August abundance estimates ranged from 77,000 to 141,000 individuals within suitable habitat. If the Two Forks Reservoir were built, approximately 21 percent of Hlm suitable habitat would be inundated, and from 23 to 42 percent of the Hlm population would be lost, inferred from the 1986 skipper density measurements.

The overall pattern of adult Hlm annual densities at the Trumbull forest thinning transects is interpreted as recovery from the 2001-2002 drought through 2007. Then density varied from year to year in response to both above and below average annual precipitation and temperature, but a general trend of increasing population size through 2021.

Forest thinning treatments that were implemented at Trumbull from 2000 through 2004 are compatible with the continued survival of the skipper. A tree thinning pattern that preserves a conifer canopy cover of approximately 30 percent and 100 trees (5 inches or greater in diameter) per acre appears optimum for maintenance of Hlm habitat.

Post-Hayman fire Hlm monitoring in moderately to intensively burned areas documents slow population recovery over time. Monitoring indicates that Hlm occurrence is negatively associated with standing dead trees, which may mean that intensively burned areas will remain sparsely inhabited over the long term. This avoidance behavior means that crown fires that kill all mature conifers represent a significant risk to the suitable habitat extent for this species.

Genetic samples from Hlm and congeners were analyzed to investigate species and subspecies relationships and determine Hlm population substructure. Analysis of cytochrome c oxidase subunit I (COI) showed *H. leonardus* haplotypes are distinct from other *Hesperia* species, but it was not possible to distinguish *H. leonardus* subspecies from one another based on the observed COI haplotypes. Population structure analysis of Hlm samples using single nucleotide polymorphism (SNP) genotyping revealed gene flow throughout the range of Hlm, but clusters of more related individuals were distinguishable along a geographic gradient from north to south. Two individuals collected 4 miles south of the 1986 study area were noticeably different in the SNP analysis. The area includes remnants of ponderosa pine forest with blue grama and dotted gayfeather that survived the Hayman Fire. More investigation is needed to determine if this finding indicates an isolated subpopulation.

Keywords: *Bouteloua gracilis,* climate change, cytochrome c oxidase I, drought, forest restoration, haplotype, *Hesperia leonardus montana*, landscape genetics, *Liatris punctata*, population monitoring, ponderosa pine ecology, single nucleotide polymorphism, South Platte River, weather, wildfire

Introduction and Overview

The Pawnee montane skipper *(Hesperia leonardus montana* Skinner, 1911) is confined to an area of less than 80 square miles within the South Platte River drainage southwest of Denver in Douglas and Jefferson Counties, Colorado. Scott and Stanford (1982) established the type locality of subspecies *montana* as Buffalo Creek, near the confluence of the North Fork of the South Platte and the main stem of the South Platte River. This skipper occupies xeric ponderosa pine woodland that has developed on soils derived from the Pikes Peak granite and is geographically isolated from populations of *H. l. pawnee*, a prairie subspecies that occurs east of the Front Range foothills.

This skipper (hereafter referred to as "Hlm") was listed as a Threatened Species in 1987 under the Endangered Species Act (Federal Register 1987) primarily because Denver Water proposed to construct the 1.1-million-acre-foot Two Forks Reservoir that would have inundated approximately 21 percent of known Hlm habitat (Shoumatoff 1986). This proposal triggered field studies (1985 through 1988) to better document Hlm habitat area, population distribution and size, as well as the direct impacts of reservoir construction (ERT 1986, 1988, 1989). This information was used to support the consultation among the federal agencies and Denver Water. The Two Forks Reservoir was denied federal approval for construction by the U.S. Environmental Protection Agency in 1990. After the federal listing, the USFWS published a Recovery Plan (USFWS 1998) that identified criteria for forest management actions that were compatible with continued Hlm survival and eventual recovery.

In 2000, the U.S. Forest Service, in cooperation with the Colorado State Forest Service and private entities including Denver Water, initiated the Upper South Platte Watershed Protection and Restoration Project that included timber harvesting, prescribed burning, reforestation of burned areas, obliteration and reclamation of unnecessary roads, and trail improvements (Culver et al. 2001). The USFS prepared a Biological Assessment to evaluate the potential effects on listed species that could be affected by this project (USDA Forest Service 2000). The Hlm was included because suitable habitat for this species was included within areas proposed for forest thinning and prescribed burning. To assist in identifying project effects over the short- and long-term, the USFS and Denver Water sponsored a Hlm monitoring program to evaluate the species' response to treated and untreated areas. Annual monitoring began in August 2000 and continued through 2021.

Four major wildfires (Buffalo Creek, Hi Meadow, Schoonover, and Hayman) burned approximately 12,000 acres of Hlm habitat within a six-year period (1996 to 2002). The largest of these, the 2002 Hayman Fire, burned over 9,000 acres within suitable Hlm habitat, of which approximately 5,000 acres were burned at a moderate to high severity (Graham 2003). After the Hayman Fire was controlled in July 2002, the federal land managers assembled a team to conduct a rapid assessment of skipper occurrence and ground cover status in low, moderately, and severely burned areas. Monitoring began in August 2002 and continued through 2018.

This Contribution summarizes field studies that have been conducted for various federal agencies and Denver Water over the past 36 years. The long period of monitoring has disclosed a range of Hlm population and understory habitat responses to forest thinning treatments and annual weather patterns. The Hlm annual population trends and local responses can be used to formulate future habitat management strategies. Rapid climate change has caused higher annual temperatures, more variable precipitation, increased number and severity of wildfires, and increased risk of seasonal droughts. The ponderosa pine woodland inhabited by the Hlm is naturally subject to frequent low- to mixed-severity fires and is fire adapted, but the risk of large, high-intensity stand-replacing fires that could burn a large fraction of the suitable habitat has substantially increased. Documenting the Hlm population responses to drought and fire are critical to understanding the long-term survival outlook for this taxon.

The specific scientific knowledge contributed by these studies is as follows:

The Two Forks Reservoir skipper field study involved a large (80 square mile) mapping effort of skipper suitable habitat (Fig. 1) combined with ground verification measurements of skipper occurrence and abundance and measurement of key habitat variables (tree and shrub overstory, larval foodplant, and adult nectar sources). These studies produced range-wide estimates of skipper abundance and habitat quality and provided essential information for assessing risk to skipper populations from habitat inundation by the proposed Two Forks Reservoir. The majority of this work was completed in the 1986 field season (ERT 1986). The belt transect sampling methods for skipper and habitat variables in this study were extended to subsequent studies (ERT 1988, 1989).

The South Platte Restoration study represents a long (21 year) monitoring record for both skipper and adult nectar source abundance. The Cheesman Reservoir meteorological station (CSU 2021, 2022) provides a site-specific source of annual temperature and precipitation data. The study period includes an extreme regional drought year (2002) that provides evidence of how well the Hlm population survived and rebounded from this climatic stress event and provides a benchmark for future droughts predicted by climate change modeling. Forest management treatments designed to improve ponderosa pine ecosystem health and resilience to climate change and wildfires are compatible with Hlm persistence.

The post-Hayman wildfire study provides a long (16-year) record for skipper population reoccupation of moderately to severely burned habitat areas, as well as the recovery of the larval foodplant and adult nectar sources. Burned habitat reoccupation data provide a basis for future species habitat management actions and recovery.

Genetic analysis of samples taken across the range of Hlm provided insight into the genetic variability of Hlm subpopulations within its known range and a basis for comparison with other *Hesperia leonardus* subspecies.

Pawnee Montane Skipper Habitat

The climate of the South Platte drainage within the study area (**Figure 1**) consists of cool but not extremely cold winters (average Cheesman Reservoir January temperature: 20^0 F) followed by warm summers (average Cheesman Reservoir July temperature: 66^0 F). Annual average precipitation averages approximately 16 inches and is highly variable in amount from year to year. The annual precipitation pattern consists of light precipitation in the form of snow from November through March, followed by a precipitation peak in April and May when the area often receives heavy snow and rain. Average monthly precipitation for April and May exceeds 1.5 inches. The area experiences a second precipitation peak in July and August when frequent thunderstorms cross the region during the afternoons that result from an influx of upper-level monsoon moisture from the southwest. Average monthly precipitation declines to 1 inch or less from September through October (CSU 2022).

The North Fork and main stem of the South Platte River form a system of deep canyons where the rivers drain east and north parallel to the Rampart Range uplift and exits the foothills of the Front Range through Waterton Canyon at approximately 6000 feet. The river cuts through layers of igneous rocks that make up the Pikes Peak Formation (USGS 1979). Within the study area, topography ranges from very steep near the confluence of the North Fork and main stem of the South Platte River, and less steep where the river valleys widen near Deckers and Trumbull on the South Fork and near Buffalo Creek and Pine on the North Fork.

Weathering of Pikes Peak Granite produces very young, unstable soil (Sphinx-Legault-Rock Outcrop map unit) consisting of coarse gravelly sandy loam (USDA Forest Service and Soil Conservation Service 1992).

This soil overlies the parent rock at depths of 6 to 12 inches. The soil layer is unstable and susceptible to landslides on very steep slopes. Intense, brief thunderstorms frequently cause substantial rill and gully erosion on sparsely vegetated slopes. The coarse sandy soil is well drained and influences the development of a vegetation community tolerant to periodic drought, as well as surface and subsurface instability caused by freeze-thaw.

Habitat for the Hlm lies within the ponderosa pine - Douglas-fir vegetation type (Kuchler 1964) that covers an extensive area of the Colorado Front Range foothills. Within the South Platte drainage between elevations of 6,000 to 7,500 feet, ponderosa pine is the dominant tree on drier slope aspects (primarily southeast through southwest). Ponderosa pine forms mixed stands with Douglas-fir on cooler (primarily northwest through northeast) slope aspects.

Ponderosa pine woodland habitat types (DeVelice et al. 1986, Hess and Alexander 1986) occupied by Hlm include the ponderosa pine/blue grama/little bluestem habitat type at lowest elevations and driest slope aspects. The ponderosa pine/mountain muhly habitat type occurs at intermediate elevations and experiences a slightly higher soil moisture regime. The ponderosa pine/bearberry habitat type occurs primarily above 7,000 feet on cooler slope exposures and represents sites near the upper elevation limit of Hlm.

The landscape patterns and fire history of ponderosa pine and Douglas-fir communities have been extensively studied around Cheesman Reservoir. The Denver Water property that includes Cheesman Reservoir was not logged or grazed after the early 1900s, and therefore provides an example site where patterns of historic forest structure have been preserved, except for forest fire suppression that began after settlement. Studies of tree age and wildfire scars (Huckaby et al. 2001) indicated that this area experienced a mixed-severity fire regime. Stand-replacing fires occurred in a range of 20 to 50 years; mean fire intervals of all intensities were approximately 10 years. Trees older than 400 years were found in 30 percent of sampled stands, indicating that numerous old growth trees have persisted into the present.

Kaufmann et al. (2001) studied fire and tree recruitment patterns around Cheesman Reservoir to assist in the development of forest restoration criteria. These researchers found that the historic forest pattern consisted of four patch conditions: openings (crown closure less than 10 percent); ponderosa pine (crown closure greater than 10 percent); ponderosa pine – Douglas-fir (crown closure greater than 10 percent); and persistent old growth (crown closure greater than 10 percent). The general recovery sequence consists of openings created by pockets of stand replacing fire; seedling establishment primarily by ponderosa pine, with density of Douglas-fir increasing over time; and long-term mature forest patches dominated by mixed ponderosa pine and Douglas-fir. Surface fires that consume understory vegetation and coarse woody debris often reduce the density of young Douglas-fir, which are less fire resistant than ponderosa pine. Based on recorded tree ages, conifer recruitment occurred in pulses separated by one or more decades.

Fire suppression and logging since the early 1900s have resulted in a change from a low canopy closure pattern (**Figure 2a**) to a much more closed-canopy, even-aged pattern. For example, photographs of Cheesman Reservoir in the early 1900s, and simulations of historic canopy cover based on tree age sampling, show that most of the area was occupied by forest stands with canopy cover of 30 percent or less, with dense stands restricted to north-facing slopes (Kaufmann et al. 2001). By 1996, most of the same area was occupied by stands with canopy closure of 30 percent or greater, with most of the stands with canopies of 30 percent or less occurring on warmer, south-facing slopes.

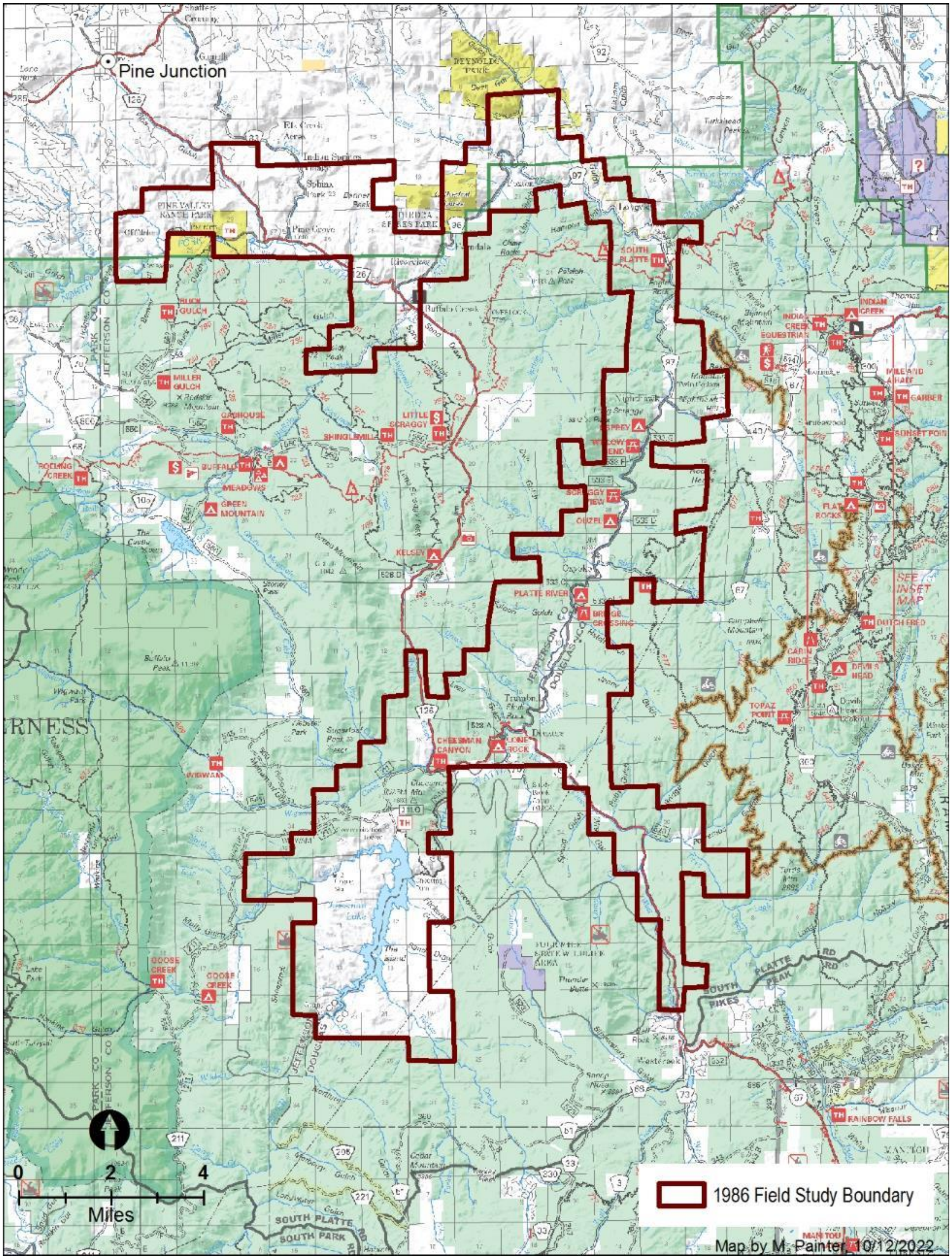

Figure 1. Pawnee montane skipper surveys, 1986 field study boundary.

Figure 2. Clockwise from top left: a) Optimal Pawnee montane skipper habitat after thinning; b) dotted gayfeather (*Liatris punctata*); c) egg (left of pen collar) of Pawnee montane skipper on blue grama (*Bouteloua gracilis*); d) adult female Pawnee montane skipper. Source: Colorado Natural Heritage Program.

In the northern part of the Hlm range, the Denver South Park Pacific Railroad constructed a narrow-gauge line up the South Platte canyon from Denver to the vicinity of Fairplay in the early 1880s. This railroad operated until 1937. The canyon slopes near the railway track were extensively logged but have now largely reforested naturally. Small communities (Buffalo Creek, Pine, Trumbull, Nighthawk) were established along the valley floors in conjunction with railroad operations. The narrow rocky canyons restricted the development of irrigated agriculture, and forest understory grasslands provided minimal forage for livestock.

Understory shrub and herb species occur at low densities within suitable Hlm habitat. The primary adult nectar source, dotted gayfeather (*Liatris punctata*), occurs as small patches in forest openings throughout the Hlm elevation range (**Figure 2b**). The Hlm larval foodplant blue grama grass (*Bouteloua gracilis*) is ubiquitous throughout the study area on warm slope exposures within ponderosa pine woodland openings (**Figure 2c**). Other species commonly associated with suitable habitat include fringed sagewort (*Artemisia frigida*), smooth yucca (*Yucca glauca*), little bluestem (*Schizachyrium scoparius*), sun sedge (*Carex inops*), mountain muhly (*Muhlenbergia montana*), and false hairy goldenaster (*Heterotheca villosa*). The Hlm is generally absent from mountain mahogany (*Cercocarpus montana*) communities, even though blue grama and dotted gayfeather are common there. (Plant names conform to Ackerfield 2022.)

Pawnee Montane Skipper Life History

The entire Hlm life cycle is completed annually (one generation per year). Adult butterflies of both sexes begin emerging in early August, but most abundantly from mid-August through early September. Adult behavior is divided among nectar feeding, mate location by both sexes, and oviposition by females (**Figure 2d**).

Adult nectar feeding is the most commonly observed behavior. There is a very strong nectaring preference for dotted gayfeather. Each year's leaves arise from a perennial woody taproot and rhizomes, which aid drought resistance (Weaver 1954). Flowering stems appear in July, and flowers begin to open in late July to early August, coinciding with the emergence of Hlm. Dotted gayfeather flowering stems are determinate, meaning that the flower buds begin opening at the stem apex, and then open successively at lower positions along the stem. Flowers are blue to purple, and nectaries are located near the base of the tubular corolla in the individual florets, which are approximately 1 cm long. Dotted gayfeather is an ideal adult nectar source because of the long flowering period (August through mid-September), and because different gayfeather clumps bloom at different times depending on slope exposure and available soil moisture.

Other nectar sources less frequently used by Hlm adults include false hairy goldenaster (*Heterotheca villosa*), smooth blue aster (*Symphyotrichum laevae*), narrow-leaved butterweed (*Senecio spartioides*), musk thistle (*Carduus nutans* – introduced species), Canadian thistle (*Cirsium arvense* – introduced species), beebalm (*Monarda fistulosa*), geranium (*Geranium caespitosum*) (Wooley et al. 1991), and smooth white aster (*Symphyotrichum porter)*, western lined aster (*Symphyotricum lanceolatum hesperium*), Bigelow's tansyaster (*Dieteria bigelovii*), and aspen fleabane (*Erigeron speciosus*) (Scott 2014). In the 2002 extreme drought, Hlm were observed moving from upland hillsides into riparian areas where nectar sources were in better condition.

In anticipation of courtship, adult males patrol around and through ponderosa pine woodland openings and often perch on dotted gayfeather stems while awaiting females. In courtship, the male overtakes the female in the air. They flutter together, with the male hovering below the female. The pair lands and the male flutters to disseminate his pheromone. A receptive female is quiescent and accepts the male (after landing, the male swings his abdomen laterally and copulation begins when the tips of the abdomens touch), whereas an unreceptive female flutters her spread wings to repel the male, then flies away. If a mating pair is disturbed, the female flies, the male dangling (Scott 2022).

Observations of female oviposition are infrequent, relative to other behaviors. Wooley et al. (1991) observed 6 Hlm ovipositions solely on blue grama at various locations in the North Fork and main stem of the South Platte River valleys between August 18 and September 10, 1987. Times of oviposition ranged from 1100 to 1300. Drummond (pers. comm.) observed 8 Hlm ovipositions on post-fire survey transects (see below) between 2004 and 2010, 7 in early September on blue grama between 1153 and 1422, and 1 on side-oats grama (*Bouteloua curtipendula*) on August 30, 2010, at 1450. MacNeill (1964) speculates that 20 ovipositions per female per day would be a large number, based on field and laboratory observations. Females typically lay one or more eggs on individual leaf blades within a blue grama patch. Females select blue grama patches in small to moderate sized openings with sun exposure during parts of the day, and some shading.

Eggs are cream-colored when laid and become more orange prior to emergence of the larva (**Figure 2c**). The first instar larva emerges from the egg and then the larva overwinters as a first or second instar. Four eggs field collected and raised in artificial conditions hatched at 8, 19, 21, and 42 days (Wooley et al. 1991). The Hlm larval field behavior has not been studied but is assumed to resemble that of other *Hesperia* species. In many species early instar larvae create shelters by silking grass leaves together. These shelters are usually at or above the base of the green leaf blades. Larvae leave shelters at night to

feed. Late instars build leaf and silk shelters near leaf bases, close to or under the ground. Pupation occurs after 5 to 6 larval instars within or outside the larval shelter. The time between pupation and adult emergence is estimated to be 20 days (MacNeill 1964).

A subspecies of the western branded skipper (*Hesperia colorado ochracea* Lindsey, 1941[1] - hereafter referred to as Hco) occurs within the same pine woodland habitat and flies during the same emergence period as Hlm (Pelham 2022). This subspecies occupies a variety of grassland, shrubland, and woodland habitats across the Colorado Front Range from Larimer County to El Paso County. Larvae are able to feed on a variety of different grass and sedge species, but primarily use sun sedge (*Carex inops*). The adult behavior of Hco is very similar to that of Hlm. Males patrol through woodland openings and frequently nectar and perch on dotted gayfeather. Field observers were trained to distinguish between the two species while monitoring transects. When the observed individual could not be identified to species, it was recorded as an unknown. Observed adult Hco were recorded on all transects sampled and were analyzed with the same statistical methods as Hlm to provide evidence of year-to-year responses by both *Hesperia* species to available habitat resources and climatic conditions.

Methods

Two Forks Reservoir Surveys

<u>Project Personnel Roles and Responsibilities.</u> The primary purpose of these field studies was to gather information to inform the Two Forks Reservoir Endangered Species Act (ESA) consultation among Denver Water, the U.S. Fish and Wildlife Service, and other involved federal and state agencies. Denver Water contracted the design and implementation of the field studies to environmental consultants Environmental Research and Technology (ERT) and Professional Entomological Services Technology (PEST). Denver Water staff conducted vegetation measurements along census transects to provide skipper habitat information.

ERT, under the direction of Scott Ellis, developed the study design and survey protocols. PEST provided field survey teams for the distribution and census surveys from 1986 through 1988. The U.S. Fish and Wildlife reviewed and approved the survey protocols, and provided agency staff for the 1986 field surveys. Key members of the federal consultation team and the field survey teams are identified in the Acknowledgements section.

<u>Habitat Suitability Map.</u> An overall habitat suitability map for the entire Hlm range was prepared by plotting all known Hlm observations on 1:24,000 color aerial photos, then developing photo-interpretation criteria used to delineate habitat areas. These criteria include:

- An upper elevation limit of 7,400 feet. This elevation boundary generally coincides with a vegetation community change in which open ponderosa woodlands show a transition toward a more closed forest canopy. This elevation also generally corresponds to the highest elevations where Hlm adults were observed during distribution surveys.
- Tree canopy cover of less than 50 percent; slope aspect generally southeast to southwest, except on slopes less than 15 percent.
- Shrub canopy cover nearly absent; ground cover consisting of grass patches (primarily blue grama and little bluestem); soil color orange to brown; large rock outcrops excluded.

[1] Synonym: *Hesperia comma ochracea* Lindsey, 1941; invalid name (Retrieved Nov. 8, 2022, from the Integrated Taxonomic Information System (ITIS) online database, www.itis.gov, CC0, https://doi.org/10.5066/F7KH0KBK

The draft habitat suitability map was verified during distribution surveys when the occurrence of Hlm, blue grama, and dotted gayfeather were recorded for each quarter section (160 acres) included in the survey. The accuracy of the map was calculated by dividing the number of quarter sections in which Hlm skippers were observed by the total number of quarter sections containing mapped suitable habitat.

Habitat and Adult Skipper Survey Design. The field survey study area consisted of 310 quarter sections (160 acres per quarter section) for a total survey area of 77.5 square miles. After the study area was defined based on Hlm habitat suitability, a stratified random sampling design was employed to collect skipper and habitat data from all parts of the study area (ERT 1986). The decision to establish multiple sampling strata was influenced by the large study area size, the complex terrain characterized by large elevation differences and multiple slope aspects, and differences in land use history. This design allowed skipper density data (skippers/acre) collected on transects to be extrapolated to estimated densities over the much larger sampling strata (**Figure 3**). Strata of varying sizes were defined to subdivide the range of the skipper outside the proposed Two Forks inundation area (Treatment A) and within the inundation area of the proposed Two Forks Reservoir (Treatment B).

Distribution Survey. The distribution survey was designed to provide information on Hlm and Hco adult density and habitat characteristics in Treatment A and B sampling areas (**Figure 3**). A pace transect sampling method was implemented to collect statistically comparable data over a large geographic area within a short sampling time period (August 14 through August 28, 1986). The pace transect technique has been widely applied in England on areas managed as butterfly preserves (Thomas 1983, Pollard 1977). These authors tested this method on several butterfly species, including *H. comma*. It was concluded the method is useful for estimating numbers of free-flying species that do not show strongly aggregative behavior or territorial defense. Same-day resampling of *H. comma* populations indicated that abundance estimates were very similar between samples. Correlations between pace census transects and coincident mark-recapture studies were not high for *H. comma*. This lack of correlation was attributed to the low recapture rate for skippers (Thomas 1983, Pollard 1977).

All field survey participants were trained to distinguish differences between Hlm and Hco from field observations and photographs. Participants walked trial transects to help standardize the walking pace and the observation area on both sides of the transect. Observers were assigned transects in both treatment areas and within different strata on each sampling day to reduce potential observer bias. Observations along the transects were completed by a team of two. An equivalent sampling effort (80 transects) was conducted within both Treatments A and B.

The sampling unit consisted of a belt transect 800 paces long and 40 feet wide within a quarter section. Each quarter section selected for sampling was further subdivided into four, 40-acre blocks. To maintain sampling efficiency, and to account for terrain variability, a 200-pace segment was sampled in each 40-acre block within the quarter section. The direction of the second segment was oriented approximately 90 degrees from the first; resulting in a box or diamond-shaped pattern after all four segments were completed.

Habitat measurements as well as skipper observations were recorded. Blooming dotted gayfeather stems were counted within the entire area of the belt transect and the presence/absence of the larval

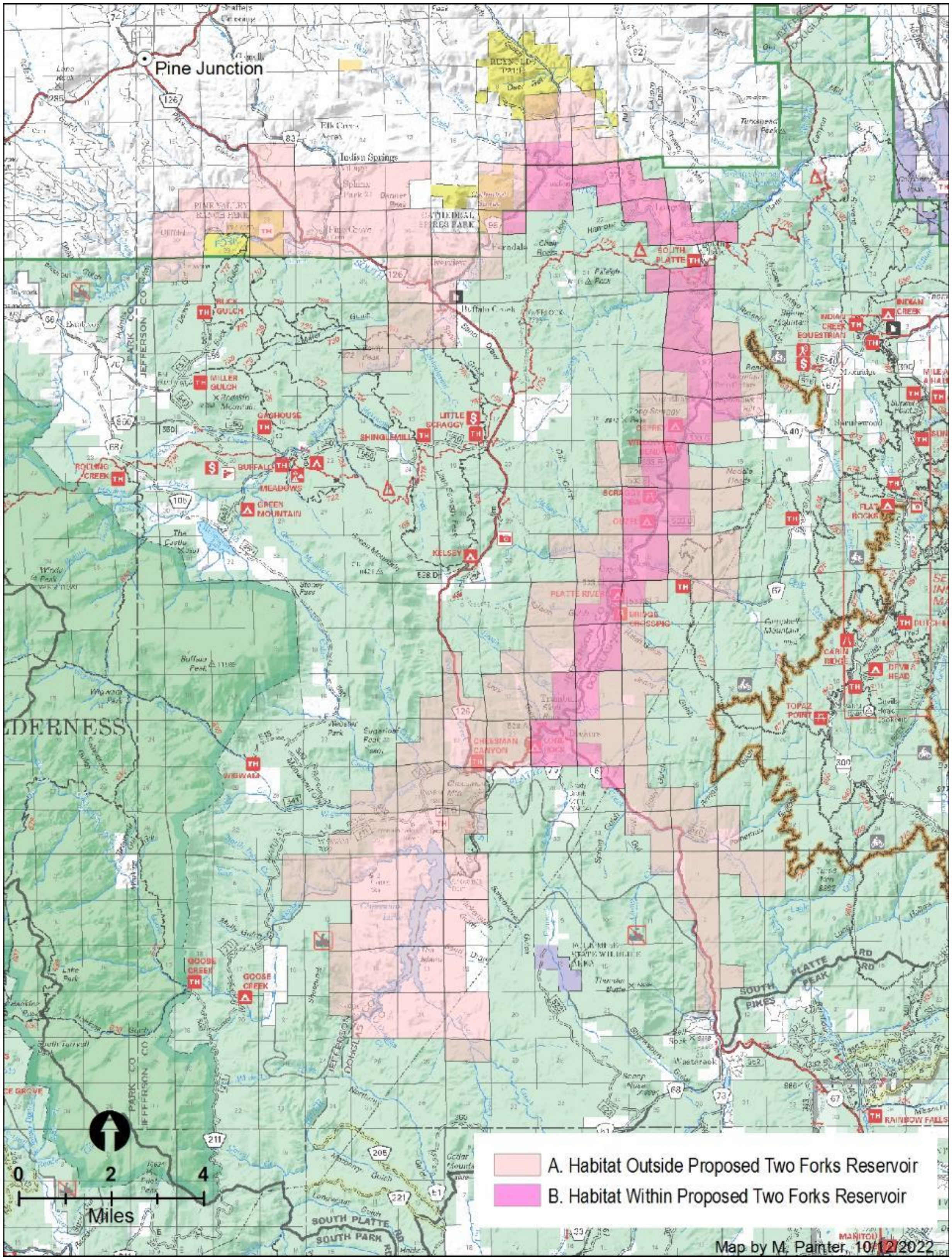

Figure 3. Pawnee montane skipper survey habitat stratification by maximum water elevation of proposed Two Forks Reservoir.

foodplant (blue grama grass) was recorded at the end of each 20-pace interval for a total of 40 points per 800-pace transect. The number of skippers (Hlm and Hco) was recorded within the entire belt transect area (20 feet on either side of the transect centerline).

Census Survey. The census survey was designed to provide detailed information on Hlm habitat within belt transects of a specified size and monitor the number of skippers and behavior within the same belt transects to develop a habitat suitability profile based on skipper use.

Similar to sampling site selection for the distribution surveys, quarter sections to be sampled were randomly selected from study area strata. A total of forty-six 400-meter by 10-meter belt transects were established across the study area (24 in Treatment A and 22 in Treatment B; **Figure 4**). Each 400-meter transect was further subdivided into sequential 50-meter by 10-meter plots. Transect endpoints were marked with permanent stakes. All transects were sampled from mid-July to early August 1986.

The following vegetation information was collected within the boundaries of each belt transect:

- Number of flowering stems of dotted gayfeather per transect.
- Percent cover of blue grama and other grass species measured in a 1-meter square plot at each 10-meter interval along the transect.
- Number of trees by size class (used to extrapolate tree density = number of stems/acre). Size measured by diameter at breast height (dbh): less than 5 inches, 5 to 9 inches, greater than 9 inches.
- Length of tree and shrub canopy intercepted by the transect centerline.

Census transects were then sampled for skipper occurrence in each 50-meter by 10-meter plot along the 400-meter transect so that relationships between habitat components and skipper occurrence could be examined and skipper abundance estimated. All census transects were sampled from August 21 through 27, 1986, and again in 1987 and 1988 during the August-September flight period (ERT 1988, 1989).

Statistical Analysis. Habitat data from census transects (tree and shrub percent canopy cover, tree density, dotted gayfeather stem density, grass and blue grama percent ground cover) were combined and averaged for the 24 Treatment A transects, and 22 Treatment B transects. The results were tabulated and statistically compared (Welch's t-test) to determine the relative habitat differences between these two treatments.

The distribution and census transect skipper occurrence data were analyzed separately in accordance with the stratified random sampling design. Each stratum was assigned a weight based on its proportion of the entire Treatment area. Weighted average of skippers/acre and weighted variance for each stratum were calculated. The weighted averages and variances were summed for all strata included within Treatment A and those within Treatment B.

Abundance estimates for each treatment area were calculated by multiplying the weighted skipper average/acre by the total number of acres included within the Treatment. Standard errors of the mean for the Treatment abundance estimates were calculated by multiplying the square root of the weighted Treatment variance by the treatment area.

A total abundance estimate for the entire study area was calculated separately for the distribution and census surveys by summing the abundance estimates from the two Treatment areas. The standard error of the mean for a total abundance estimate was calculated by taking the square root of the sum of the weighted Treatment variances multiplied by the Treatment areas squared.

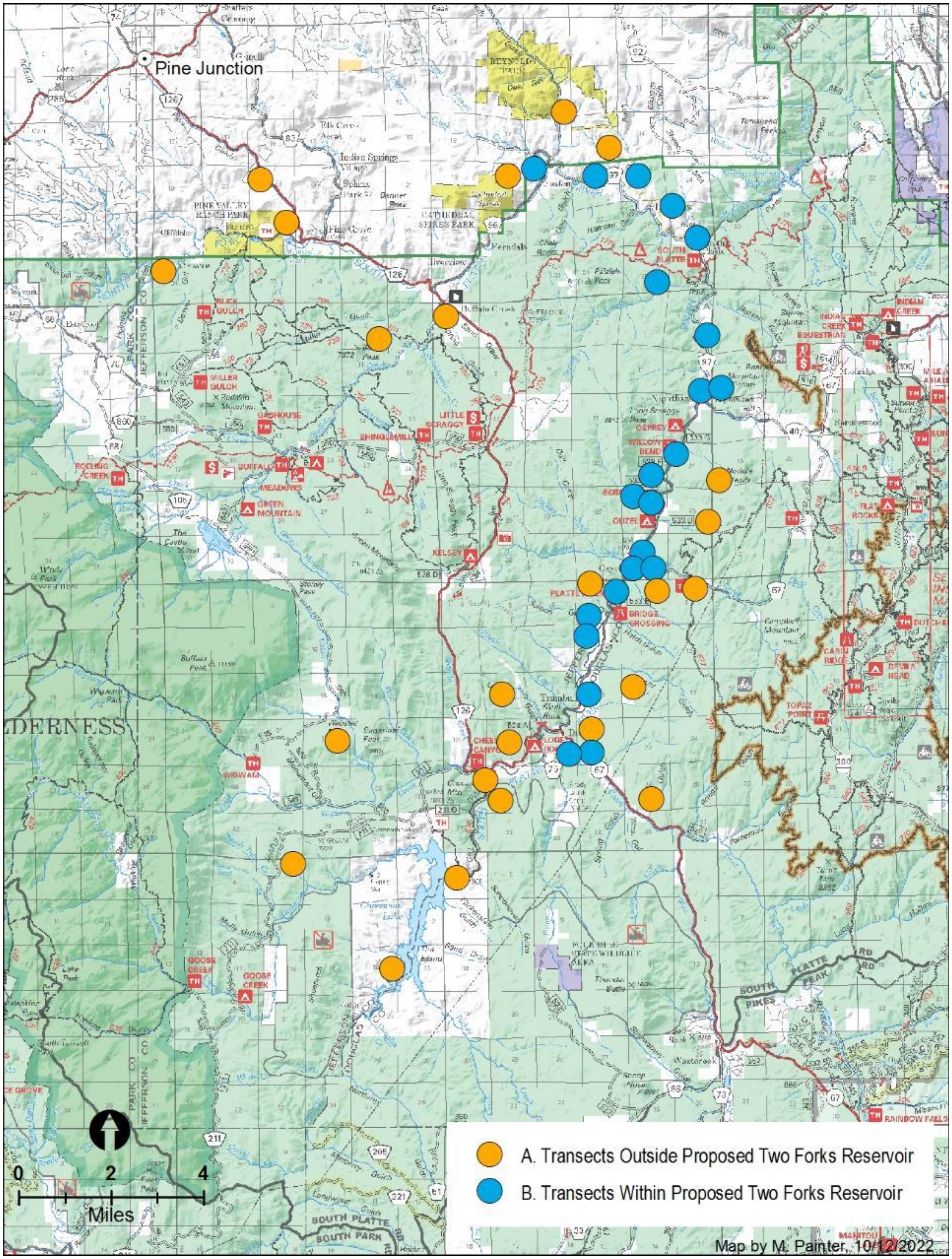

Figure 4. Pawnee montane skipper census transects relative to maximum water elevation of proposed Two Forks Reservoir.

Upper South Platte Watershed Restoration Project Surveys

This monitoring study (ENSR 2001) was designed to compare the number of adult *Hesperia* skippers within four forest treatments including three areas that received substantial thinning in either 2000 (2000 Treatment Area), 2002 (2002 Treatment Area), or 2004 (2004 Treatment Area) and a Control Area located along the South Platte River near Trumbull, Colorado (**Figure 5**). The Control Area approximates optimal skipper habitat characteristics described by the U.S. Fish and Wildlife Service (USFWS 2001)**.** Monitoring has been completed annually starting in 2000 (ENSR 2000, 2001, 2003a,b; Drummond 2004, 2005, 2007, 2008, 2009, 2010; Sovell 2012, 2013b, 2014a, 2015b, 2016, 2017b, 2018a, 2019b, 2020a, 2021, 2022a).

The 2000 and 2002 treatments consisted of selectively thinning young and mature ponderosa pine trees so that the resulting mature tree density of approximately 100 mature trees per acre was relatively homogeneous across the stand and overall tree canopy cover ranged from 30 to 40 percent. One small clearcut patch of approximately two acres is included in the 2000 thinning treatment. The 2004 treatment was thinned more intensively than the previous treatments, and consisted of intervals of narrow clearcut strips, as well as thinning within the adjacent forest to a level similar to that of the 2000 and 2002 treatments. Merchantable timber was removed, and residual harvest slash and other debris were either burned in piles or chipped on site. No logging roads remain in these thinned areas.

Project Personnel Roles and Responsibilities. Denver Water requested that ENSR (formerly ERT) prepare a study plan to evaluate relative skipper use of treated and untreated pine woodlands. ENSR, under the direction of Scott Ellis, initiated the first field surveys in 2000. Other participants included staff from Denver Water, the USFWS, and USFS. ENSR conducted surveys and prepared survey reports for three years (2000 through 2003). The program was then passed to the Colorado Natural Heritage Program, under the direction of Boyce Drummond and John Sovell. USFS staff (Denny Bohon, Steve Culver, Mike Elson, and Mikele Painter) sequentially assumed agency leadership for the monitoring project. The USFS and CNHP staff formed a core of experienced observers who trained USFS seasonal employees and volunteers from various organizations.

A detailed sampling protocol (Drummond 2004) was developed for field participant training at the beginning of each field day. Experienced observers were paired with less experienced participants to reduce errors in skipper identification, and to ensure that flowering Liatris stems were counted consistently from year to year.

Field Surveys. The monitoring procedure involved counting all *Hesperia* skippers including Hlm and Hco along permanently marked 400-meter by 10-meter belt transects. Each transect was sampled three times within the flight season of Hlm. The abundance of the primary adult nectar source (dotted gayfeather) was measured by counting the number of flowering stems present within each belt transect and the abundance of the larval food plant (blue grama) was measured by noting its presence or absence at subplots within each monitored transect. Annual and growing season (March – August) mean temperature and precipitation were collected from the nearby Cheesman weather station and compared to their 25-year means from 1985-2009.

Statistical Analysis. An analysis of variance was conducted after each monitoring year to determine whether there were significant differences in the skipper counts among treatments (Control Area, 2000 Treatment Area, 2002 Treatment Area, and 2004 Treatment Area) within and across the 15 monitored transects. Similar statistical analyses of blooming dotted gayfeather stems were performed.

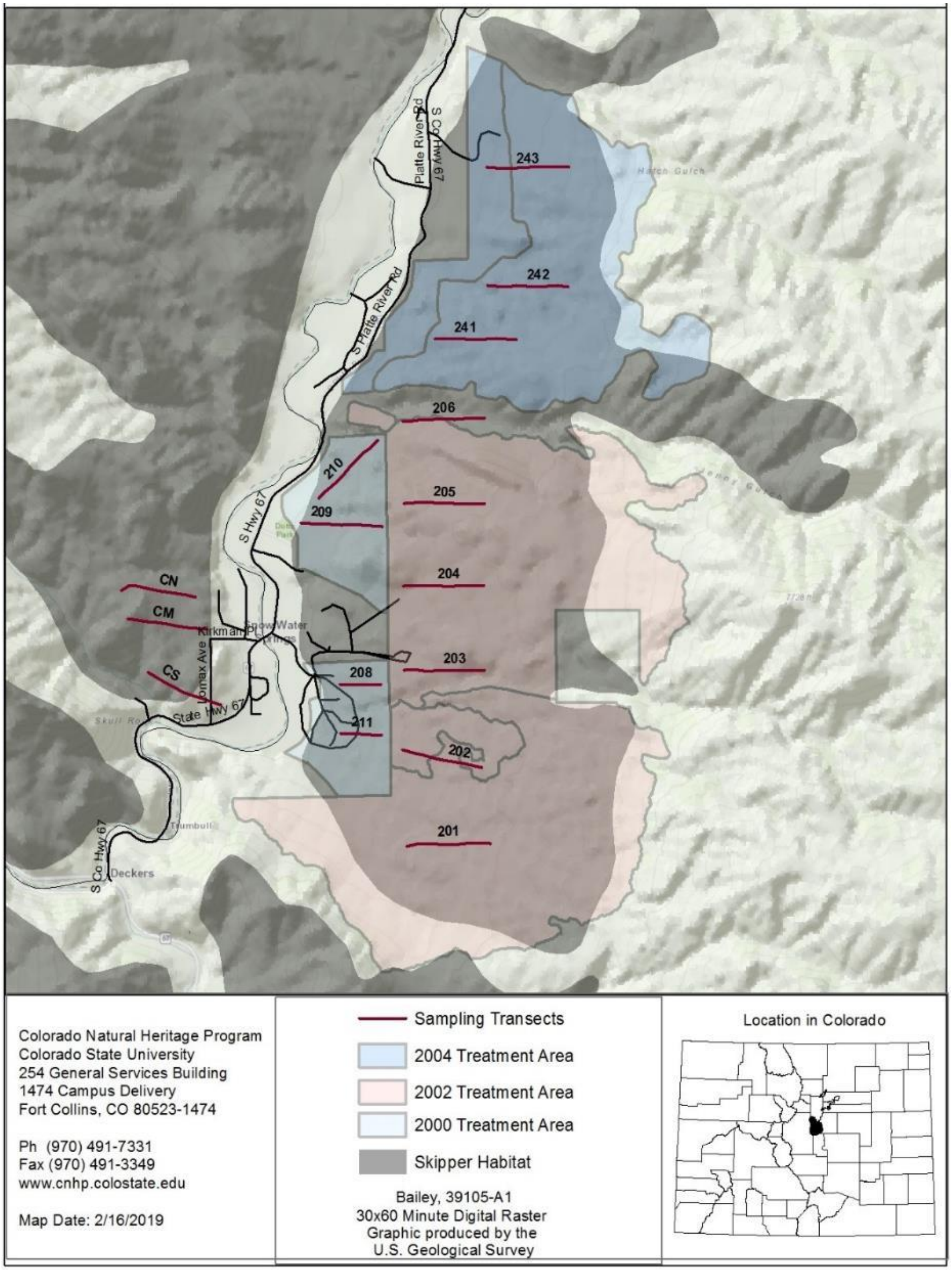

Figure 5. Pawnee montane skipper monitoring transects in the vicinity of Trumbull, Colorado. Trees were mechanically thinned by different treatments in different years; Control area (CN, CM, CS) was not thinned.

Multiple regression was also performed to understand how precipitation, temperature, and dotted gayfeather are associated with skipper density and how precipitation and temperature are associated with dotted gayfeather density among treatments. The following variables were analyzed:

- Hlm per acre (dependent variable),
- flowering stems of dotted gayfeather per acre,
- mean annual and growing season temperature,
- deviation of mean annual and growing season temperature from the 25-year mean,
- mean annual and growing season precipitation, and
- deviation of mean annual and growing season precipitation from the 25-year mean.

Post-Wildfire Surveys

This monitoring study was designed to evaluate how wildland fire has influenced the relative size and extent of Hlm populations. The primary objective of this study was to compare skipper use (measured by the number of adult butterflies seen within a known area) of burned and unburned ponderosa pine forest within the Hayman Fire area. Sampling was initiated in 2002 (ENSR 2003c), the year of the Hayman and Schoonover fires (Graham 2003) and continued for the next two decades (CNHP 2005; Sovell & Drummond 2006; Sovell 2007, 2009, 2010b, 2011, 2013a, 2015a, 2017a, 2019a;).

USFS delineated the burn severity classes on the appearance of the burned and unburned trees on satellite and aerial photo imagery and through subsequent field surveys assessing accuracy of the mapping effort (**Figure 6**). The skipper habitat sampling data collected in 2002 verified the USFS burn severity map (U.S.D.A. Forest Service 2002). The map was quite accurate in depicting the condition of the overstory trees. Since stands classified as high or moderate burn severity were associated with an understory that was nearly always 100 percent burned, it seemed most appropriate to analyze these transects together because in 2002 there was no skipper occupancy of these areas and overstory recovery will require many years.

The low severity burn class includes a mosaic of unburned and partially to completely burned trees, with both burned and unburned understory patches. Because there was a potential that some skippers still occupied these low severity burn areas immediately following the burn in 2002, and some overstory trees remain, it is likely that skipper abundance differs from that in high-to-moderate severity burn areas. Consequently, transects located within low burn severity areas mapped by the USFS were analyzed as a single group. Thus, in the Hayman fire area, there were transects distributed among three burn classes: unburned, low severity burn, and moderate-to-high severity burn (**Figure 7**).

Project Personnel Roles and Responsibilities. The USFWS and USFS requested that ENSR prepare a rapid-assessment study plan to estimate effects on skipper populations immediately after the 2002 Hayman Fire was controlled. The field team consisted of staff from ENSR, CNHP, and the USFS.

Field Surveys. A stratified random sampling approach was employed to select sampling locations to assure that skipper and habitat data were collected from all parts of the study area. A total of eighty-three 800-meter by 10-meter transects were established across the study area of which 56 were sampled in 2002. Although the number and identity of each transect surveyed has varied during the period of monitoring, since 2007 the same 32 transects have been sampled for the most part (**Figure 6**).

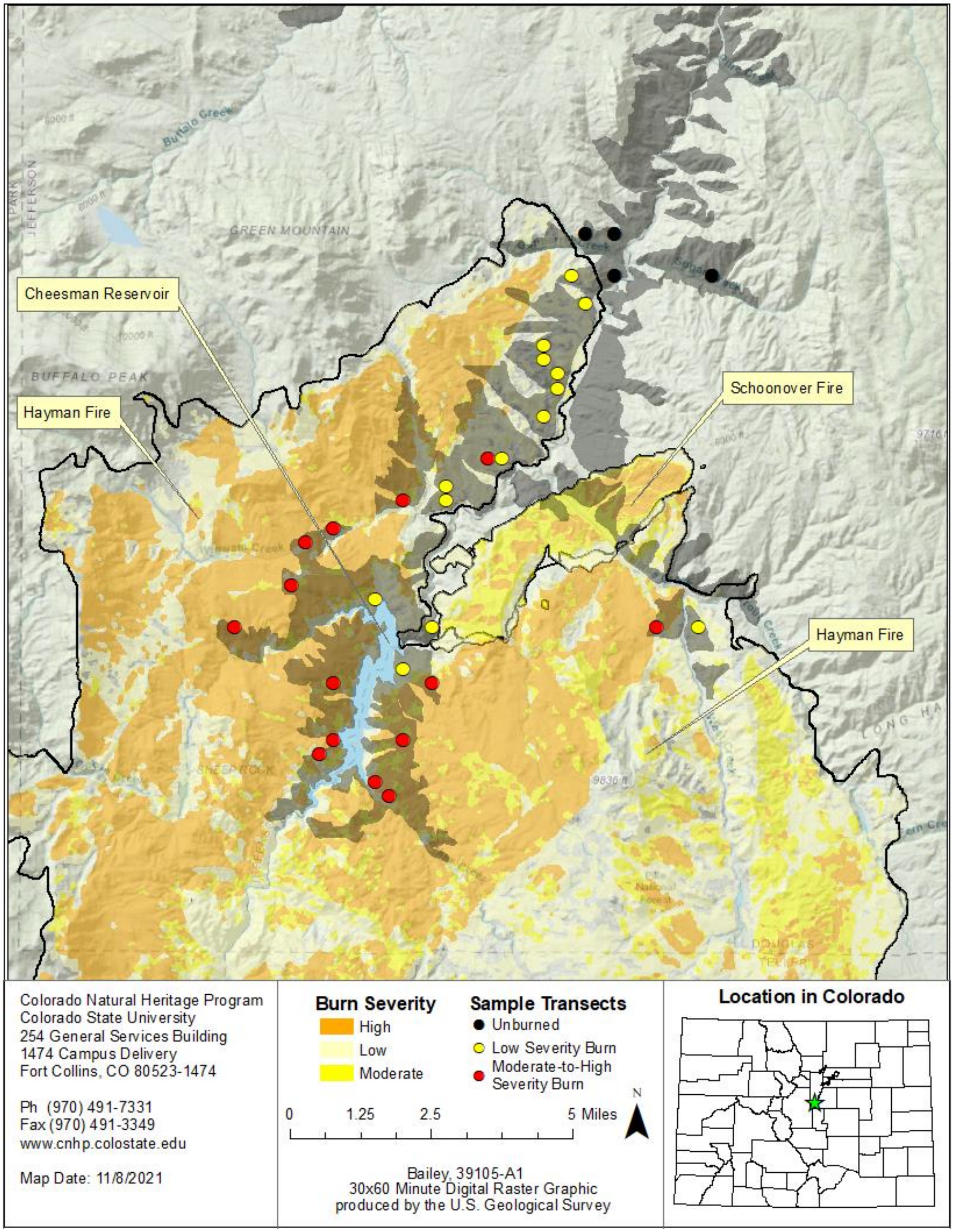

Figure 6. Pawnee montane skipper habitat burned by the Hayman and Schoonover fires and locations of the 32 post-fire skipper monitoring transects sampled since 2007.

Figure 7. Photo representation of the burn severity classes: top photo - an unburned transect; middle photo – a low severity burn transect; bottom photo – a moderate to high severity burn transect. Source: Colorado Natural Heritage Program

The field sampling methods used for this monitoring study (ENSR 2003c) are similar to those used for the 1986 Hlm Two Forks Reservoir distribution survey. A detailed survey protocol was prepared that specified the use of GPS units to establish transect start and end points that could be sampled in future years. Photos were taken periodically along transects to document forest burn conditions. Staff training followed the procedures outlined in the protocol.

The sampling unit consisted of a belt transect 10 meters wide and 800 meters in length that was divided into four 200-meter segments. Each 200-meter segment was further divided into ten 20-meter intervals. Each transect was based on a standard starting point and at the end of each 200 meters, the next segment was oriented 90 degrees to the right of the just completed segment. This resulted in a transect that was a geometric box or diamond with the final 200-meter segment ending at or near the transect's original standard starting point.

The monitoring procedure involves counting all *Hesperia* skippers including Hlm and Hco. The abundance of the primary adult nectar source (dotted gayfeather) was measured by counting the number of flowering stems present within each belt transect; the abundance of the larval food plant (blue grama) was measured by noting its presence/absence in a one square meter quadrat at the end of each 20-meter interval. Live and dead trees 6 inches dbh and greater within the belt transect were counted during the first 10 years of the monitoring effort. Annual and growing season (March – August) mean temperature and precipitation were collected from the nearby Cheesman weather station and compared to their 25-year means from 1985-2009 (CSU 2021, 2022).

<u>Statistical Analysis.</u> A two-factor analysis of variance was conducted after each monitoring year to determine whether there were significant differences in the skipper and vegetation variables among burn classes (Unburned, low severity burn, and moderate to high severity burn) within and across the monitored years.

As the monitoring effort progressed, and with every addition of annual data, the analysis of variance lost statistical power. As a result, there were few significant differences detected in Hlm densities between burn areas within each year. Logistic regression is better suited for handling multi-year datasets without loss of power. Additionally, some variables have not changed appreciably among burn areas during all the years of monitoring. The occurrence of blue grama has never shown a difference among burn areas, and the data have always shown significantly more live trees and fewer dead trees on unburned and low severity burn areas than moderate-to-high severity areas, as expected. Therefore, analyses of variance for live trees, dead trees, and frequency of blue grama in relation to burn area were removed from the analysis. Prior to turning to logistic regression to analyze the data, the following 8 variables were analyzed using a two-factor analysis of variance:

- Hlm per acre (dependent variable),
- flowering stems of dotted gayfeather per acre,
- live and dead trees per acre,
- mean frequency of blue grama grass,
- annual and growing season temperature,
- annual and growing season precipitation,
- the burn intensity experienced by the plots, and
- the distance each burned transect was located from unburned suitable Hlm habitat.

Multiple Linear Regression and Modeling. All years of monitoring data were analyzed using multiple regression analysis to look for correlations and potential causal relationships between weather variables, skippers, and gayfeather counts. The statistical significance of the goodness-of-fit measure (r^2) for the linear regression was calculated. This statistic indicates the percentage of the variance in the dependent variable that the independent variables explain collectively. R-squared measures the strength of the relationship between the model and the dependent variable on a 0 – 100% scale.

All years of monitoring data were also analyzed using logistic regression models, Akaike's information criterion (AIC), and multi-model inference to investigate how densities of Hlm were influenced by biotic and abiotic habitat factors. The data were analyzed using logistic regression (R Development and Core Team 2016). The analyzed models were compared using Akaike's information criterion for small sample sizes (Burnham and Anderson 2002). Models were ranked using AIC_c weights (w_i), unconditional parameter estimates (β_i) were calculated for each variable, and 95% confidence intervals pertaining to each variable's parameter estimate were calculated. Variables with 95% confidence interval around β_i that do not overlap zero have a strong effect in explaining model variance (Burnham and Anderson 2002).

Five biotic variables were modeled including:

- the density of dotted gayfeather per acre,
- frequency of blue grama,
- density of dead trees per acre,
- density of live trees per acre, and
- the severity of burn that the transect experienced during the Hayman Fire of 2002.

Five abiotic variables were modeled including:

- growing season precipitation,
- annual precipitation,
- growing season temperature,
- annual temperature, and
- the distance each burned transect was located from unburned suitable Hlm habitat.

Results and Discussion

Two Forks Reservoir Surveys

Analysis of 1986 data focused on similarities and differences in Treatment A and B habitat components and skipper densities. This information was used to evaluate the extent and quality of suitable habitat that would be lost and remain, and the fraction of the Hlm population that would be lost and remain in the event the reservoir was constructed. To predict remaining adult skipper densities after the construction of Two Forks Reservoir, the 1986 census transects (ERT 1986) were monitored again in 1987 (ERT 1988) and 1988 (ERT 1989) in Treatment A sampling strata only.

Habitat Suitability Map. The 1986 distribution surveys were conducted in 159 quarter sections, representing approximately 50 percent of quarter sections available for sampling within the study area. An error analysis of the draft habitat suitability map showed that actual Hlm occurrence was 72 percent of the quarter sections mapped as suitable habitat; dotted gayfeather occurred in 96 percent of suitable habitat quarter sections. Blue grama, the Hlm larval foodplant, occurred in nearly every survey transect. Highest predicted/actual occurrence percentages for both Hlm and dotted gayfeather were observed around Cheesman Reservoir; lowest skipper percentages were observed in the vicinity of Pine. In summary, the 1986 habitat suitability map (**Figure 8**) and associated photointerpretation criteria provided a reliable basis for predicting the extent of suitable habitat and occupation by Hlm over the entire study area. This map represents the habitat that was present prior to the Hayman Fire in 2002.

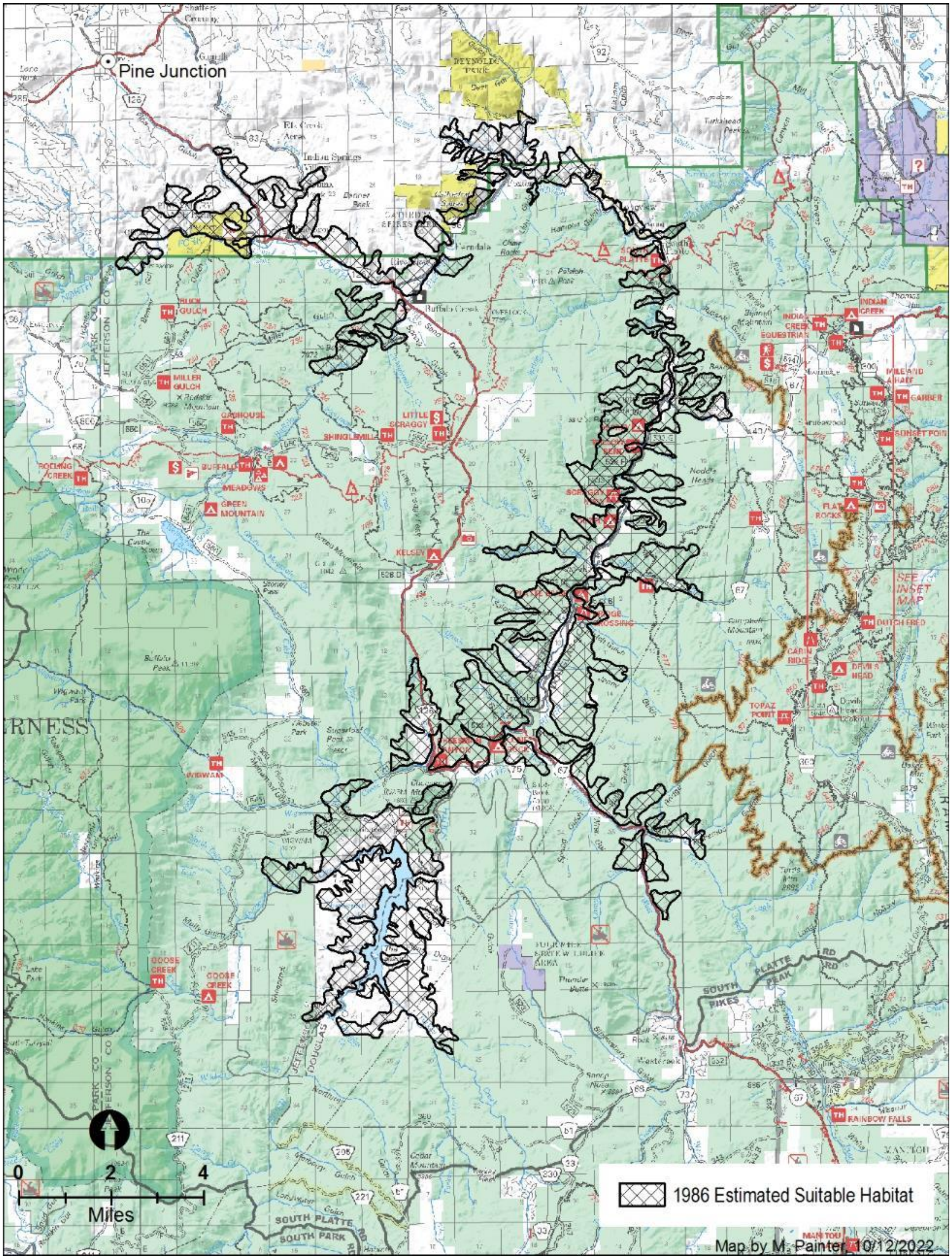

Figure 8. Pawnee montane skipper estimated suitable habitat per 1986 surveys.

Hlm Habitat Characteristics. Table 1 provides a comparison of the Hlm habitat components sampled on 1986 census transects in Treatments A and B. Means and variances were compared using Welch's t-test.

Table 1. Habitat characteristics of 1986 census transects located outside (Treatment A) and inside (Treatment B) the proposed Two Forks Reservoir inundation boundary.					
Vegetation Component-1986 Measurements	Mean of Treatment A transects (N=24)	Standard Error of the Mean	Mean of Treatment B transects (N=22)	Standard Error of the Mean	Statistical Significance (P=.05)
% canopy cover					
Tree	33.13	1.91	29.41	2.23	NS
Ponderosa pine	22.63	2.37	22.05	1.98	NS
Douglas-fir	9.33	1.81	6.82	1.24	NS
Shrub	5.96	1.40	10.59	2.60	NS
% ground cover					
Grass	7.58	0.70	11.23	1.52	S
Blue grama	1.96	0.30	2.68	0.45	NS
Flowering Stems/Acre					
Dotted gayfeather	35.95	7.66	300.70	139.02	S
Tree density/acre					
All trees 0 to 5 inches	191.75	28.86	118.03	17.64	S
Ponderosa pine 0 to 5 inches dbh[1]	63.92	9.72	76.63	17.30	NS
Douglas-fir 0 to 5 inches dbh	108.86	25.74	35.23	8.07	S
All trees >5 to 9 inches dbh	55.59	6.48	38.86	5.86	S
All trees > 9 inches dbh	47.60	4.30	38.86	6.70	S
[1]dbh = diameter breast high					

Hlm abundance estimates. Table 2 provides estimates of Hlm density/acre, abundance within Treatment areas, and overall study area abundance resulting from summation of the Treatment area density estimates for the distribution and census surveys. Skipper densities measured on the

distribution transects were similar for both Treatments; skipper densities measured on the census transects were substantially greater in Treatment B.

Table 2. Hlm abundance estimates from 1986 distribution and census surveys			
	Treatment A (Outside Two Forks Reservoir boundary)	Treatment B (Inside Two Forks Reservoir boundary)	Total
Distribution Survey (N=159)			
Mean Hlm/acre	1.5336	1.7126	
Acreage	38,720	10,400	49,120
Abundance Estimate	59,379	17,811	77, 191
Standard Error	8,767	3,145	9,314
Percent of Suitable Habitat	79	21	
Percent of Overall Hlm Abundance	77	23	
Census Survey (N=46)			
Mean Hlm/acre	2.1163	5.4464	
Acreage	38,720	10,880	49,600
Abundance Estimate	81,942	59,257	141,199
Standard Error	21,578	12,269	24,822
Percent of Suitable Habitat	79	21	
Percent of Overall Hlm Abundance	58	42	

Dotted gayfeather and adult skipper counts were recorded in 400-meter Treatment A census transects established in 1986 within the same August time period over three sequential years to provide a baseline abundance estimate in the event that the Two Forks Reservoir was constructed (**Table 3**). The number of gayfeather flowering stems significantly increased (p=.05) over the three-year period. Only the Hlm density increase between 1986 and 1988 was significant at p = 0.10.

As indicators of soil moisture and vegetation growth conditions, water year precipitation (October 1 to September 30 of the following year) was below average in 1986, and above normal in both 1987 and 1988. 1986 winter season precipitation was in the range of two to three inches less than subsequent years. Growing season precipitation (April through September) was above 10 inches in all three years.

Figure 9 summarizes the overall results of the 1986 field data collections. Each square mile where Hlm adults were recorded within at least one quarter section is coded in green; square miles where no skippers were recorded are coded in black. This figure documents that the Hlm skipper population occurs throughout its entire suitable habitat, with no large areas of intervening unsuitable habitat that could create subpopulation isolation.

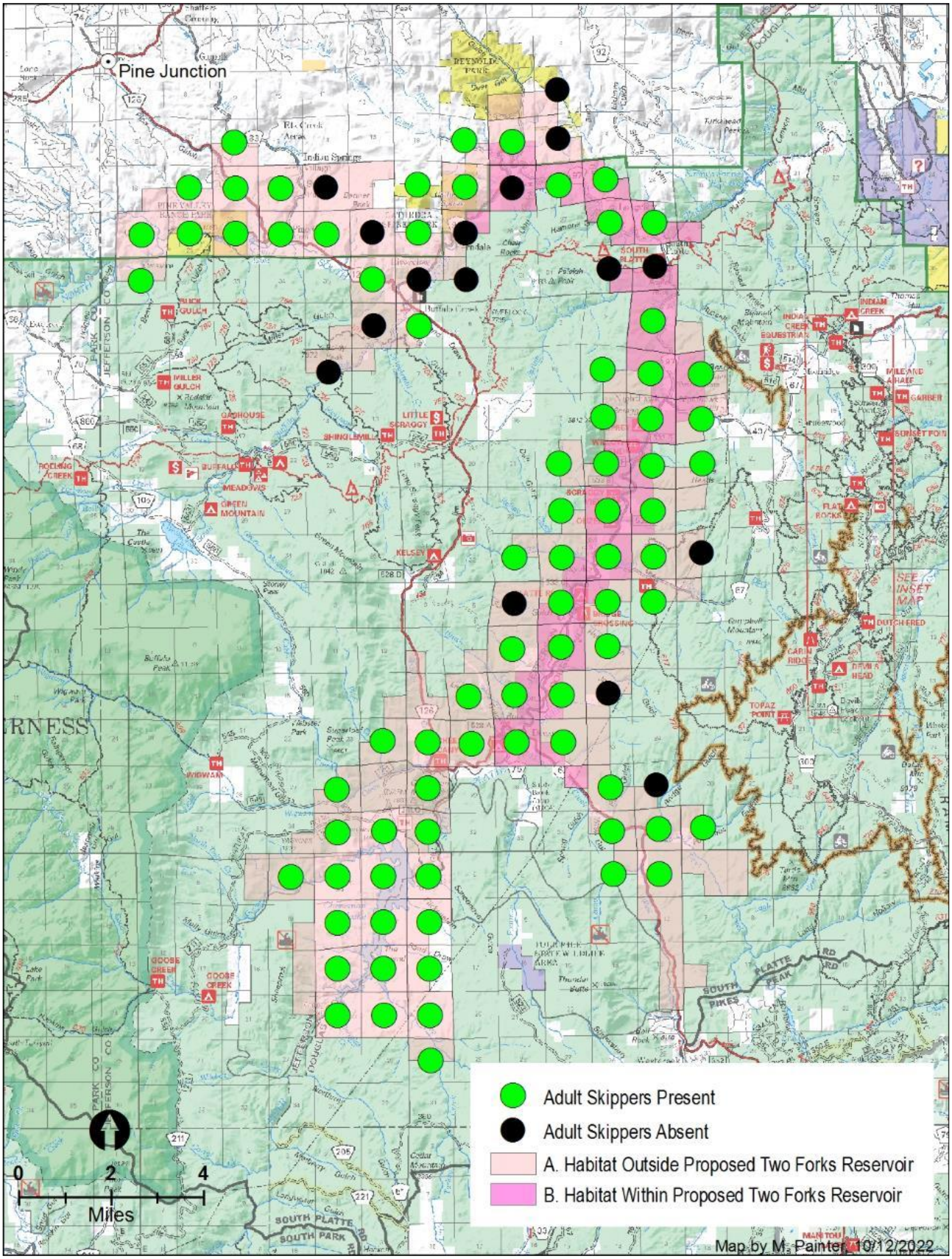

Figure 9. Pawnee montane skipper 1986 occurrences and habitat relative to proposed Two Forks Reservoir.

Discussion – Hlm Habitat, Abundance and Distribution

The 1986 vegetation measurements confirm that Hlm inhabits woodlands with sparse (30 percent) tree canopy cover dominated by ponderosa pine, and where shrubs represent a minor component (**Table 1**). Grass ground cover is low (7 to 11 percent ground cover), which includes blue grama (2-3 percent ground cover). The density of small (< 5 dbh) and larger trees (5 to 9, and >9 inches dbh) were significantly higher on the Treatment A transects. Small Douglas-fir (<5 inches dbh) density was significantly higher on Treatment A transects. Dotted gayfeather densities were significantly higher on Treatment B transects. These vegetation differences may reflect different climatic regimes because of the differences in elevation between the Treatment B census transects on the river valley floor, and the Treatment A census transects at higher elevations on the valley side slopes. The Two Forks Reservoir would have inundated elevations between approximately 6,000 feet and 6,300 feet; the Treatment A transects were located at elevations from 6,300 to 7,400 feet. Land use differences may also have contributed to these observed differences. Six Treatment A census transects were located around Cheesman Reservoir, where no timber harvest has occurred for nearly 100 years. Conversely many the Treatment B transects were located along the North Fork and the main stem South Platte Rivers, where timber stands were historically logged. In summary, the habitat components of Hlm suitable habitat are currently similar throughout the skipper elevation range, but higher elevation sites are likely to shift toward mixed stands of ponderosa pine and Douglas-fir in the future because of the large number of small (<5 dbh) Douglas-fir trees.

The distribution survey skipper densities/per acre in Treatment A and B were similar (**Table 2**). Census survey skipper densities in Treatment B were much higher than Treatment A, and higher than belt transect densities recorded in later year studies. This density difference may be the result of the smaller census survey sample size, and higher variance. It may also reflect an actual population distribution difference, in which Hlm individuals aggregated at lower elevations seeking nectar and moisture. The 1986 field measurements provided an average abundance estimate for Hlm that ranged from 77,000 adult skippers (distribution survey sampled from August 14 through 28) to 141,000 individuals (census survey sampled August 21 through 27) within its overall suitable habitat. If the Two Forks Reservoir were built, approximately 21 percent of the Hlm suitable habitat would be inundated, and from 23 to 42 percent of the skipper population would be lost, inferred from the 1986 skipper density measurements.

Dotted gayfeather and Hlm densities were measured in the same Treatment A transects for three sequential years (1986 through 1988) (**Table 3**). The significant increase in dotted gayfeather from 1986 through 1988 is attributed to above-average precipitation in 1987 and 1988, with adequate rainfall during the growing season to stimulate flowering stem emergence. Hlm showed much smaller changes in density over time. These results mirror those recorded during the 21-year habitat and Hlm monitoring conducted as part of the Upper South Platte Restoration program.

No other *Hesperia* population field studies have been conducted within study areas of this large size, likely because other rare *Hesperia* occur in small remnant habitat areas within larger fragmented landscapes. For example, the Dakota skipper (*H. dakotae*) occurs in tall grass prairie remnants within farmland in the northern Great Plains and southern Canada (USFWS 2018). The focus of much of the research on the Dakota skipper has been on the distribution of metapopulation habitats and the linkages among them that allow genetic interchange. The USFWS has not determined a minimum viable population size for this species. Dana (1991) estimated a total annual metapopulation size of 2,000-3,000 adults for a site in Minnesota. Across a 500-hectare (1,236 acre) series of prairies in southern Manitoba, a metapopulation of 2,000 individuals was estimated (COSEWIC 2014).

Davies et al. (2005) identified 257 breeding populations of *H. comma* in southern Britain in 2000. Of this number, one population was evaluated as very large (50,000 individuals at peak emergence); 3 populations were evaluated as large (3,000 to 50,000); and 17 populations as medium (500 to 3,000). All remaining populations were classified as small (less than 500 individuals). The total habitat area in Britain occupied by this species increased from less than 1 square mile to 8 square miles between 1982 and 2000. This increase was attributed to natural range expansions into suitable habitats, new human-assisted introductions into suitable habitat, and changes in grazing practices that favored the larval foodplant.

Table 3. Treatment A dotted gayfeather flowering stem densities/acre; Treatment A Pawnee montane skipper densities/acre and abundance estimates; and Cheesman Reservoir water year and seasonal precipitation. (1986 through 1988)

Year (Number of Samples)	1986 (N=24)	1987 (N=30)	1988 (N=30)
Dotted gayfeather (stems per acre)			
Mean/ Standard Error of the mean	37.49/1.51	379.84/3.65	430.21/6.04
Pawnee montane skipper (skippers per acre)			
Mean Density per Acre/ Standard Error of the Mean	2.1/0.113	3.00/0.141	3.64/0.163
Abundance Estimate From Census Surveys / Standard Error of the Mean	81,942/21,578	116,392/ 30,065	141,003/34,766
Precipitation (inches) at Cheesman Reservoir [1]			
Water Year precipitation (inches) Average: 15.78 inches	14.56	19.36	17.70
Winter Season precipitation (October - March)	3.86	6.95	6.25
Growing Season precipitation (April - September)	10.70	12.41	11.38
[1] Colorado Climate Center, Colorado State University (2001, 2002)			

Upper South Platte Watershed Restoration Project Surveys

The data collected during this study provide opportunities to: 1) to determine the overall response of the monitored skipper abundance (skippers per acre) to annual temperature and precipitation variability over the period 2000 to 2021; and 2) to determine effects from forest thinning on skipper populations over the monitoring period 2010 to 2021.

Weather Conditions and Skipper Abundance. Baseline climatic conditions for this study are the 1985-2009 monthly and annual means for both precipitation and temperature recorded at the nearby Cheesman Reservoir weather station (**Figures 10 and 11**). Growing season is defined as the period from March through September.

Over the sampling period from 2000 to 2021 skipper densities significantly increased in both the pooled *Hesperia* sample (r^2=0.44, p=0.001) and the Hlm sample (r^2=0.38, p=0.007) (**Figure 12**). The linear trend lines over the entire study period for both growing season and annual precipitation are displayed.

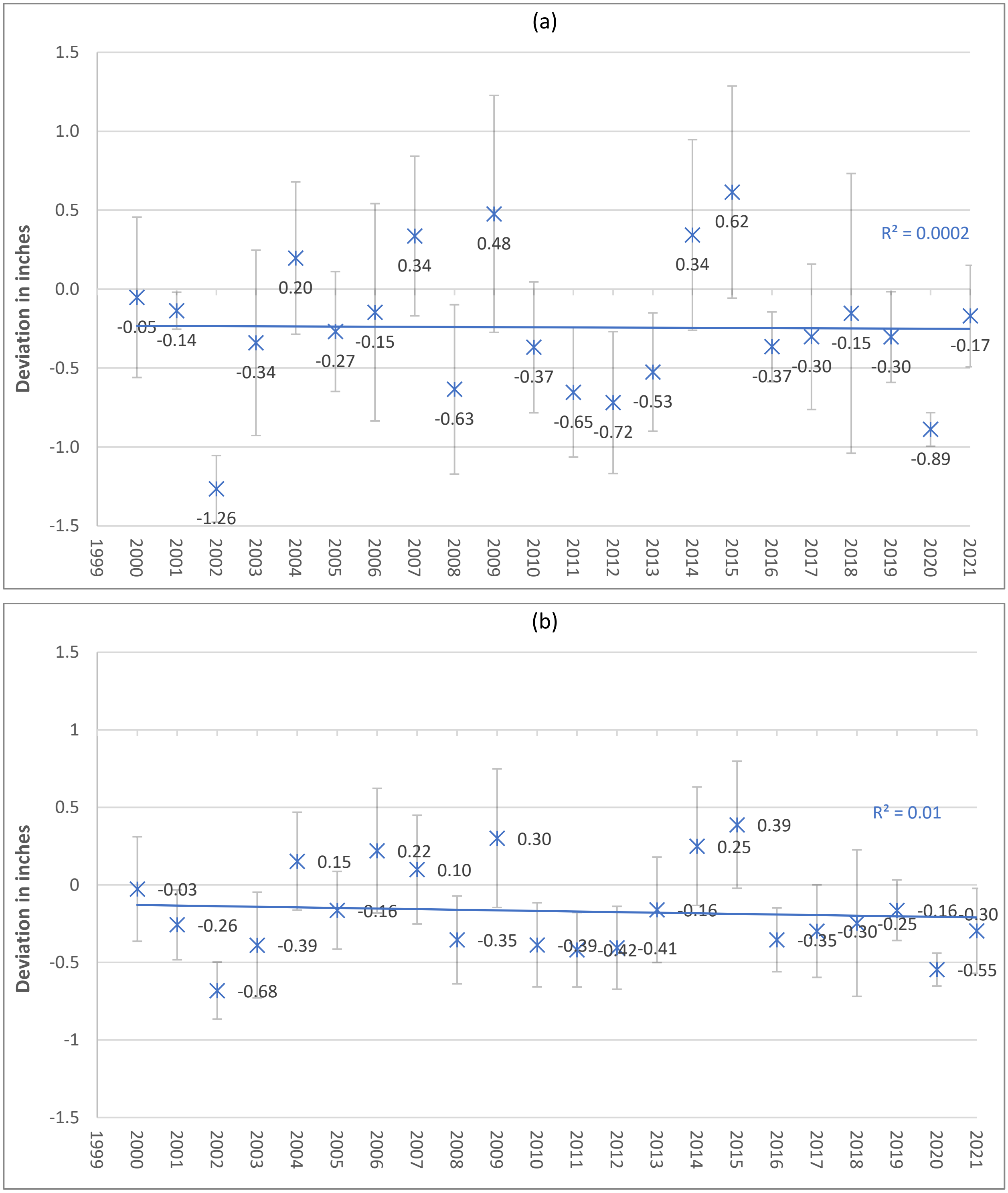

Figure 10. Deviations from mean values of (a) growing season precipitation (inches + 1 SE) and (b) annual precipitation (inches + 1 SE degrees F + 1 SE) with the 25-year mean calculated from the period 1985-2009 using data from Cheesman Reservoir weather station (CSU 2020, 2021) shown on each graph as 0.

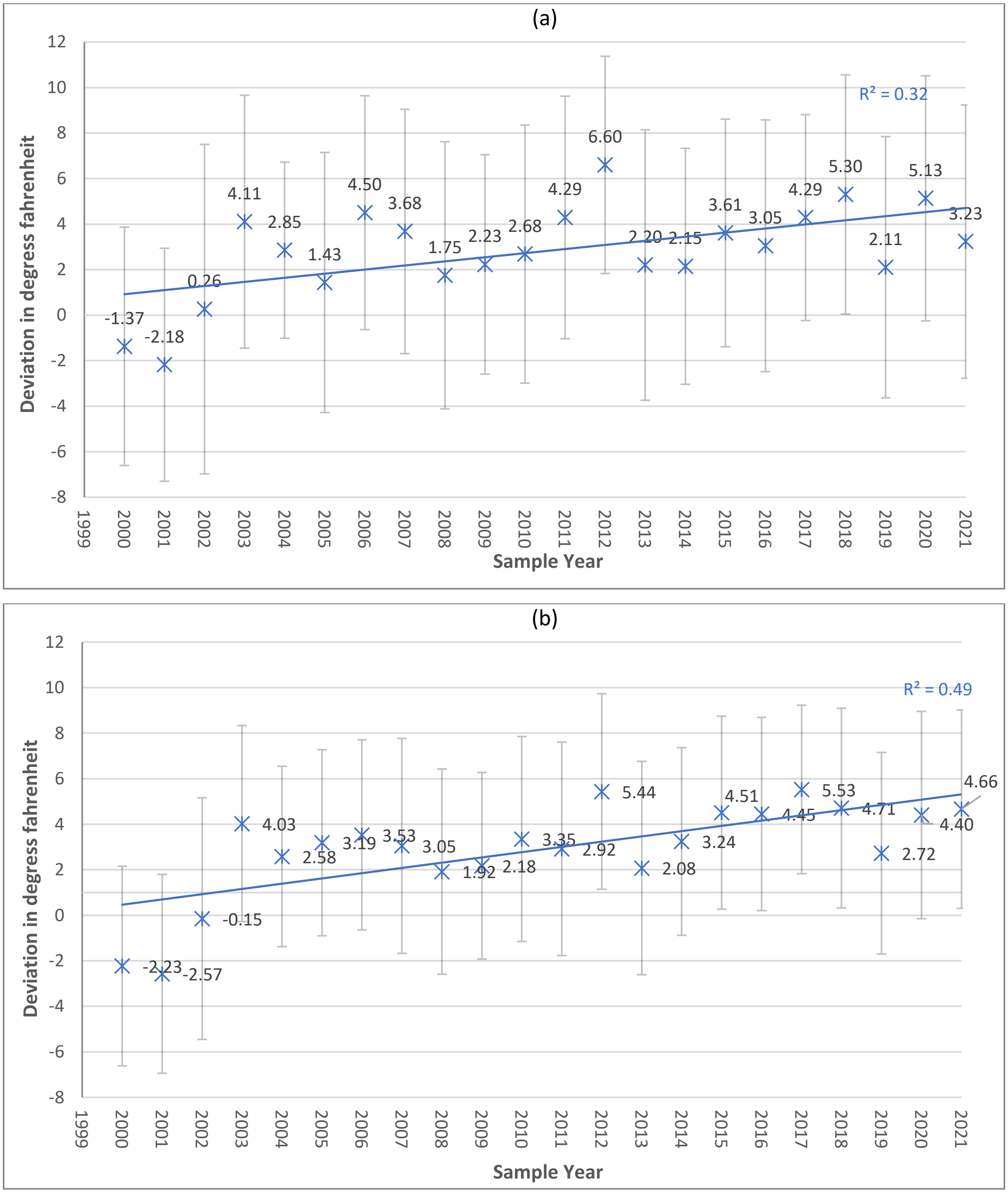

Figure 11. Deviations from mean values of (a) growing season temperature (degrees F + 1 SE) and (b) annual temperature (degrees F + 1 SE) with the 25-year mean calculated from the period 1985-2009 using data from Cheesman Reservoir weather station (CSU 2020, 2021) shown on each graph as 0.

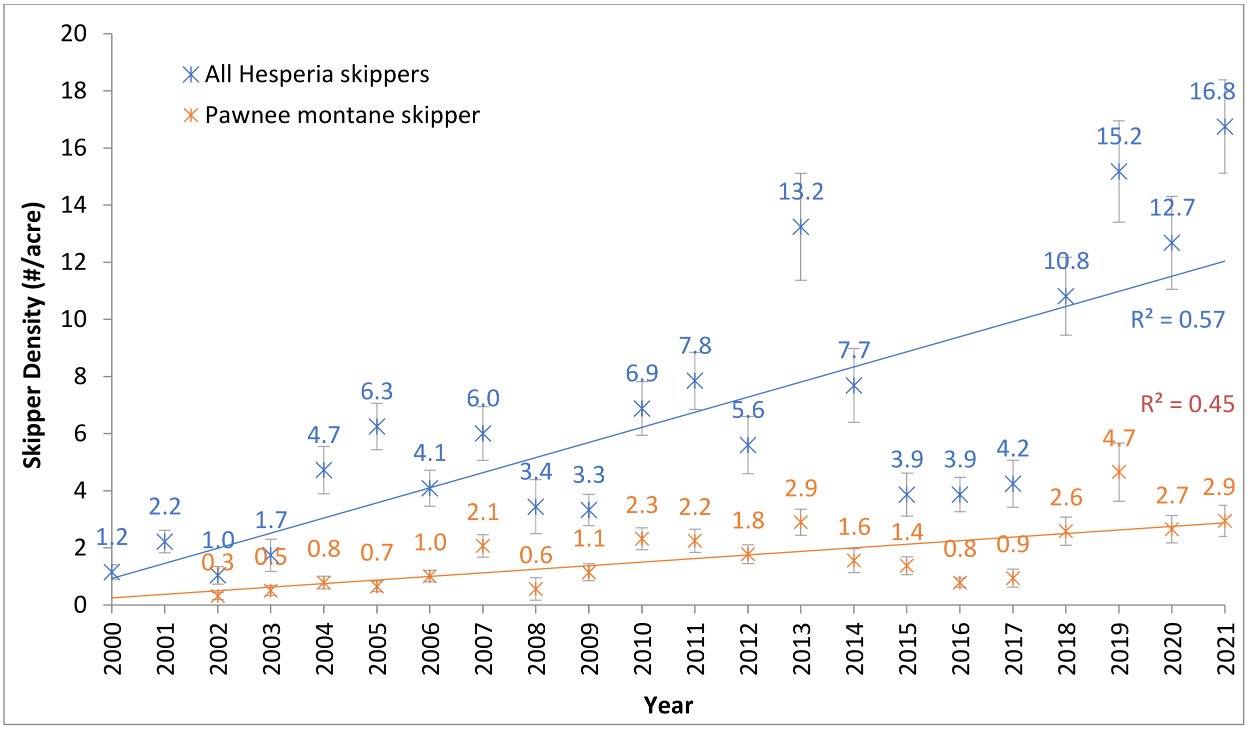

Figure 12. Comparisons of skipper (*Hesperia* and Hlm) densities across time, averaged for all forest treatments.

Discussion – Weather Conditions and Skipper Responses

Effects of Precipitation. Measures of growing season precipitation (GSP) over the monitoring period have been below the 25-year mean for most years sampled (17 of the 22 sample years). There has been a statistically insignificant decreasing trend in GSP since 2000 (r^2=0.0002, p=0.9). If the outlier value for GSP in 2002 is removed, when precipitation was 1.26 inches below the 25-year mean, then a greater portion of variation in the decline in GSP is explained by year (r^2=0.04), although it still insignificant (p=0.4).

The growing season statistics presented in **Figures 10a and 11a** do not account for weather conditions that precede the growing season. Fall, winter, and early spring precipitation builds up growing season soil moisture to support blue grama grass green-up. Near-surface soil moisture may also serve to reduce desiccation of first and second instar Hlm larvae overwintering in blue grama patches. The accumulated precipitation was examined for the interval of October through May in each year for the 2000-2019 period at Cheesman Reservoir (CSU 2022). The extremely low fall, winter, and early spring precipitation recorded from October 2001 through May 2002 represents a unique outlier relative to all the same monthly intervals in this period of record. The mean October-May 2000-2019 precipitation over the 19-year period is 7.45 inches; the precipitation for 2001-2002 was 3.16 inches, or 42% of the long-term mean. Only a trace of moisture was recorded for April. This extreme precipitation deficit set the stage for the major Hayman wildfire that started in June 2002. This fire killed mature pine trees around Cheesman Reservoir that had survived previous fires for 300 years or more (Graham 2003).

Hlm and Hco densities in the Trumbull transects monitored in August 2002 were the lowest ever recorded (**Figure 12)**. It was observed that Hlm and Hco adults were found near, or in the riparian zone along the South Platte River where nectar sources were available; no adults were observed in upland pine woodlands on the Trumbull transects, nor on the unburned post-fire transects elsewhere in the South Platte drainage in the same year. Hlm and Hco survived this extreme short-term drought and recovered to densities comparable to those measured in the 1980s.

Over longer time periods, linear multiple regression indicates that annual precipitation has a weak, negative effect on the size of skipper populations in this study area. Since relationships between precipitation and skippers are somewhat weak and inconsistent, temperature seems to be the more dominant weather factor affecting Hlm and all *Hesperia* densities.

Effects of temperature. The values of GST over the monitoring period have been above normal for most years sampled (20 of the 22 sample years). Temperatures have been trending up since 2000 and this increase is statistically significant (r^2=0.4, p=0.005) (**Figure 11a**). The values of AT over the monitoring period have been above normal for most years sampled (19 of the 22 sample years). Temperatures have been trending up since 2000 and this increase is statistically significant (r^2=0.5, p=0.0003) (**Figure 11b**).

Regression analysis shows a significant increase in skipper density in relation to increasing growing season temperatures over time. This result corresponds to the positive relationships between temperature and butterfly density that are reported in the scientific literature (Stewart et al. 2020, Kuussaari et al. 2016, Radchuk et al. 2013, Ashton et al. 2009). The benefits of increased growing season temperature may include advanced phenology and green-up in the spring, providing post-diapausal larvae with an immediately available food source; a warmer and longer adult emergence period which may increase the number and duration of reproductive activities (higher mating frequencies, a greater number of eggs per female); greater productivity of the larval foodplant as a food source, and basal leaf cover for overwintering larvae; and greater abundance of nectar sources, especially dotted gayfeather.

Unlike GST, regression analysis show that mean annual temperature has a negative relationship with the density of Hlm and all *Hesperia* observations across all forest treatments. As noted under precipitation,

the combination of drought and high temperatures outside the growing season may negatively affect the survival of diapausing larvae, including winter larval desiccation, and delays in green-up during the early spring months in the absence of precipitation. The biology of blue grama may contribute both positively and negatively to larval survival in the spring. Blue grama is a warm season grass (C4) that typically begins leaf growth in April and continues to grow vegetatively and flower in late summer. A key characteristic of blue grama is that it is extremely sensitive to adequate soil moisture for leaf growth and will remain dormant in the spring if insufficient moisture is received (Anderson 2003). Blue grama was almost entirely dormant when observed by author Ellis in the Trumbull area in early June of the 2002 drought year.

Forest thinning treatment influences on skipper and dotted gayfeather densities. The sampling results portrayed for the period in **Table 6** (skipper densities) and **Table 7** (dotted gayfeather stem densities) represent habitat occupation trends from 5 to 10 years after thinning treatment, followed by understory recovery.

Year and treatment comparisons indicate that there are no statistically different Hlm density differences across treatments and the control over the entire period. When Hlm and Hco densities are pooled, the 2018 and 2019 *Hesperia* densities in the Control treatment were significantly higher than the 2004 treatment. In 2021, the *Hesperia* densities were significantly higher in the 2000 treatment than the 2002 and 2004 treatments, but not different from the Control.

There has been no general trend over time in the density of flowering dotted gayfeather stems on any of the forest treatments; rather, density has fluctuated greatly (**Figure 13**). The main, discernable pattern is that dotted gayfeather density is positively correlated with growing season precipitation (r^2=0.3, p=0.009) and has increased dramatically in some of the wetter years, especially on the 2000 Treatment Area, with a peak of 1,377 flowering stems/acre in 2007 and 1,358 flowering stems/acre in 2009. From 2000 through 2008, dotted gayfeather plants were monitored only by counting the number of flowering stems on the transects, not the number of plants. Starting in 2009, the flowering stems counts continued but in addition a separate count was made of the number of plants on these transects. In 2009, these counts of plants did not distinguish between those with flowering stems and those without. Beginning in 2010, flowering and non-flowering plants were counted separately. For the years with data on the total number of flowering plants, there has been no significant change in the percentage of flowering dotted gayfeather plants at any of the forest treatment areas (linear regression, all $r^2 < 0.2$; all $p > 0.1$).

Table 6. Comparisons of the pooled *Hesperia* densities and the Pawnee montane skipper densities within each year, among treatment areas[1].

	Pooled *Hesperia* Sample (*Hesperia colorado* and *Hesperia leonardus montana*)				Pawnee Montane Skipper Sample (*Hesperia leonardus montana*)			
	Mean Number of Skippers per Acre P = 0.05[2]				**Mean Number of Skippers per Acre** P = 0.05[2]			
Year	**Control (N=9)[3]**	**2000 Treatment (n=9)**	**2002 Treatment (N=18)**	**2004 Treatment[4] (N=9)**	**Control (N=9)[3]**	**2000 Treatment (n=9)**	**2002 Treatment (N=18)**	**2004 Treatment[4] (N=9)**
2010	7.31 A	7.99 A	7.2 A	4.72 A	4.05 A	2.59 A	1.69 A	1.57 A
2011	11.35 A	9.22 A	7.36 A	3.94 A	4.16 A	3.15 A	1.69 A	0.56 A
2012	12.7 A	7.08 A	3.04 A	2.14 A	4.50 A	2.14 A	0.84 A	0.56 A
2013	25.74 A	15.29 AB	9.56 B	6.07 B	5.40 A	3.48 A	2.53 A	0.56 A
2014	16.75 A	8.66 AB	5.85 AB	1.35 B	3.71 A	1.57 A	1.24 A	0.00 A
2015	8.54 A	4.5 A	1.69 A	2.92 A	3.48 A	1.24 A	0.39 A	1.35 A
2016	5.85 A	5.85 A	2.7 A	2.25 A	1.46 A	1.12 A	0.62 A	0.11 A
2017	7.87 A	3.94 A	4.1 A	1.24 A	3.15 A	0.22 A	0.62 A	0.11 A
2018	21.13 A	8.21 AB	9.50 AB	5.73 B	6.18 A	1.46 A	1.91 A	1.46 A
2019	25.18 A	18.66 AB	12.59 AB	6.86 B	12.03 A	4.05 B	2.70 B	1.80 B
2020	8.77 A	17.65 A	11.47 A	14.05 A	4.39 A	2.81 A	2.25 A	1.57 A
2021	18.1 AB	27.65 A	14.56 B	8.88 B	3.49 A	5.17 A	2.59 A	0.90 A
Grand Mean	14.11 A	11.22 A	7.47 B	5.01 B	4.67 A	2.42 B	1.59 BC	0.88 C

[1] Control Area, 2000 Forest Treatment, 2002 Forest Treatment, and 2004 Forest Treatment in the vicinity of Trumbull, Jefferson and Douglas Counties, Colorado. Upper South Platte Watershed Restoration Project.

[2] Compare the treatment areas within each year by reading the rows horizontally. Tukey's Mean Comparison Test: means (number of skippers per acre) with the same letter are not statistically different at the given probability level. [*e.g.*: for Year 2010, skipper densities are not significantly different between treatments at P=0.05 level (**A**). For 2019, Pawnee montane skipper densities at the control area (**A**) were greater than at the other three treatment areas (**B**)].

[3] Sample size (*n*) refers to the number of transects in each treatment area multiplied by 3 samples each per year.

[4] 2004 Treatment Area was first sampled in 2005.

Table 7. Comparisons of dotted gayfeather (*Liatris punctata*) flowering stem densities by year among treatment areas[1].

	Mean # flowering dotted gayfeather stems/acre[2] P =0.05[3]			
Year	**Control(N=9)[4]**	**2000 Treatment (n=9)**	**2002 Treatment (N=18)**	**2004 Treatment (N=9)**
2010	130.8 A	837.4 B	321.6 A	253.6 A
2011	60.7 A	473.1 A	132.2 A	261.3 A
2012	62.1 A	280.2 A	132.5 A	159.5 A
2013	156.5 A	477.5 A	190.2 A	203.7 A
2014	147.0 A	441.1 A	197.0 A	201.0 A
2015	111.6 A	471.5 A	167.4 A	169.3 A
2016	130.2 A	194.6 A	277.7 A	276.1 A
2017	37.8 A	50.2 A	154.8 A	266.1 A
2018	56.3 A	44.2 A	77.2 A	117.7 A
2019	99.5 A	552.1 A	195.1 A	202.0 A
2020	67.4 A	95.8 A	41.1 A	60.0 A
2021	184.1 A	336.6 A	165.4 A	135.9 A
Grand Mean	103.67 A	354.52 B	171.02 A	192.2 A

[1] Control Area, 2000 Forest Treatment, 2002 Forest Treatment, and 2004 Forest Treatment in the vicinity of Trumbull, Jefferson and Douglas Counties, Colorado. Upper South Platte Watershed Restoration Project.

[2] Compare the treatment areas for each year by reading the columns horizontally.

[3] Tukey's Mean Comparison Test: means (number of skippers per acre) with the same letter are not different at the given probability level. For example, the 2011 dotted gayfeather count means on all four treatment areas are not significantly different from each other at P=0.05 (**A**).

[4] Sample size (*n*) refers to the number of transects in each treatment area sampled three times per year.

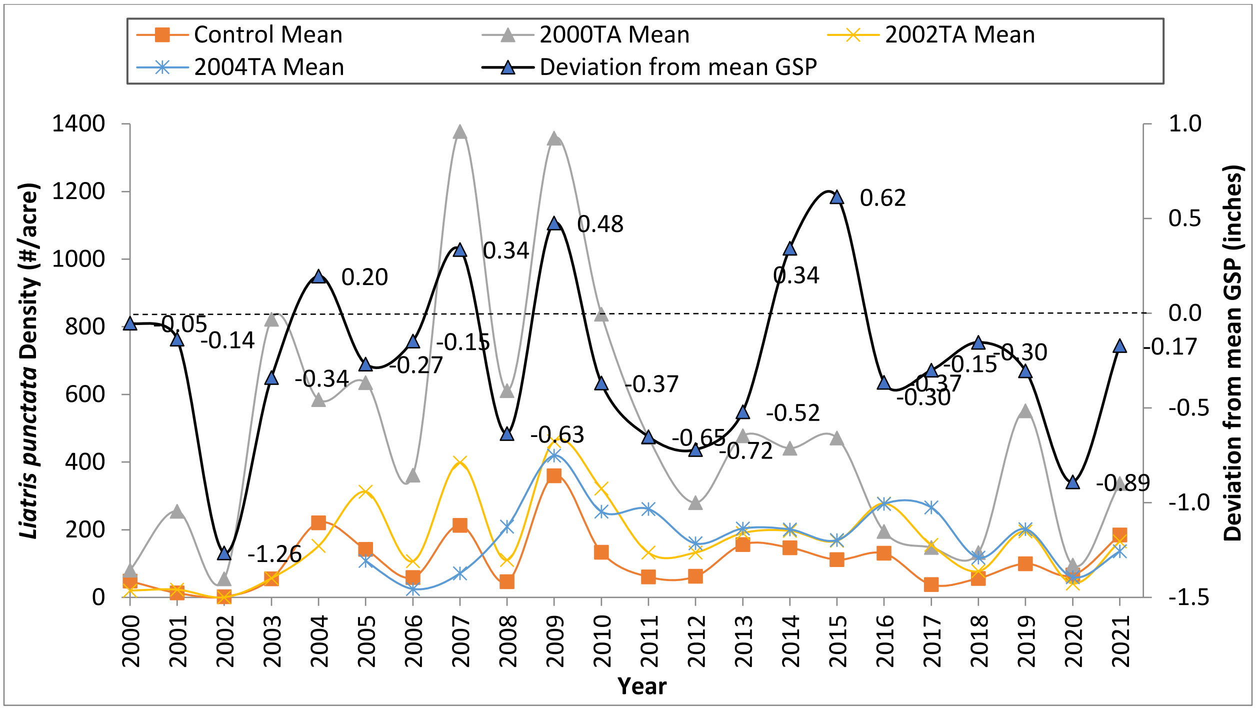

Figure 13. Dotted gayfeather flowering stem densities for all treatment areas and for all years monitored (see Table 7). The deviation from mean growing season precipitation in inches is included on the right axis for comparison. Mean growing season precipitation is calculated from the period 1985 -2009 using data from the Cheesman Reservoir weather station.

Discussion – Forest Thinning Influences

Although not statistically significant, skipper densities have been consistently lower at the 2004 Treatment Area throughout the period of monitoring. The large areas of open canopy and greater ground cover of shrubs created by the more aggressive thinning prescription applied to the area in 2004 has created a microclimate and vegetative structure that is evidently less suitable for *Hesperia* skippers (**Figure 14**). In contrast, densities of dotted gayfeather have been consistently lower at the Control Area in recent years, yet the Control Area consistently held the greatest densities of skippers. The environmental characteristics of the Control Area including forest canopy cover, tree basal area, dotted gayfeather abundance, the availability of blue grama grass, and particularly solar radiation influenced by the terrain's aspect (east facing) are likely all interacting to create niche spaces that are particularly suitable for *Hesperia* skippers (Ashton et al. 2009, Sovell 2014b, Illan et al. 2010, Yamamoto et al. 2007).

Figure 14. Example of a clear-cut opening created by the thinning prescription on Transect 242 in the 2004 Treatment Area.

Nearly 20 years of Hlm monitoring suggest that promoting variability in forest structure by creating a mosaic of forested patches and openings of approximately 0.1 acre in average size are most beneficial for Hlm population maintenance and growth (Sovell 2014). Forest thinning treatments should focus on reducing the continuity of surface and ladder fuels, while simultaneously seeking a broader ecosystem response by creating more small forest clearings and inducing positive changes in understory cover, thus benefiting both wildlife and forest hydrologic function (Lowe 2005, Waltz and Covington 2001).

Post-Wildfire Surveys

Table 8 documents skipper densities measured within unburned (control), low burn (understory partially burned, tree overstory remained), and moderate to high intensity burn (understory completely burned, tree overstory partially or entirely burned) since the 2002 Hayman wildfire. **Figure 15** visually illustrates the pattern of Hlm post-fire recovery.

Table 8. Hlm per acre by burn class[1] and total Hlm per acre.

Year	Number of Transects Sampled[2]	Burn Severity						Means Total Hlm/ Acre	Homogeneous Groups[3] (P=0.05)
		Unburned		Low		Moderate-to-High			
		Means	Homogeneous Groups[3] (P=0.05)	Means	Homogeneous Groups[3] (P=0.05)	Means	Homogeneous Groups[3] (P=0.05)		
2002	55	0.08	A	0.00	A	0.00	A	0.02	A
2003	56	0.18	A	0.08	A	0.00	A	0.08	A
2004	46	0.87	A	0.66	A	0.00	A	0.50	AB
2005	53	1.65	AB	1.22	A	0.08	A	0.94	B
2006	31	1.01	A	0.68	A	0.12	A	0.51	AB
2007	32	1.65	AB	0.83	A	0.65	A	0.85	AB
2008	32	1.52	AB	0.87	A	0.90	A	0.96	AB
2009	32	1.52	AB	1.05	A	0.51	A	0.87	AB
2010	32	4.43	B	3.43	B	0.84	A	2.38	C
2012	32	0.89	A	1.45	A	0.33	A	0.89	AB
2014	32	2.53	AB	1.27	A	0.22	A	0.97	B
2016	32	0.51	A	0.47	A	0.25	A	0.38	AB
2018	32	2.28	AB	1.45	A	0.43	A	1.11	B
Grand Mean	497	0.85	AB	0.66	A	0.29	A	0.6	AB

[1] Areas that were unburned (Control), low severity burned, and moderate to high severity burned in the vicinity of Trumbull, Jefferson and Douglas Counties, Colorado.

[2] 800m diamond-shaped transects each sampled 1 time per sample year.

[3] Compare the treatment areas for each year by reading the columns vertically. Tukey's Mean Comparison Test — means (number of skippers per acre) with the same letter are not different at the probability level indicated (e.g., See (A) and (B) for the unburned transects: 2002 is not different from 2005, and 2005 is not different from 2010, but 2002 is different from 2010).

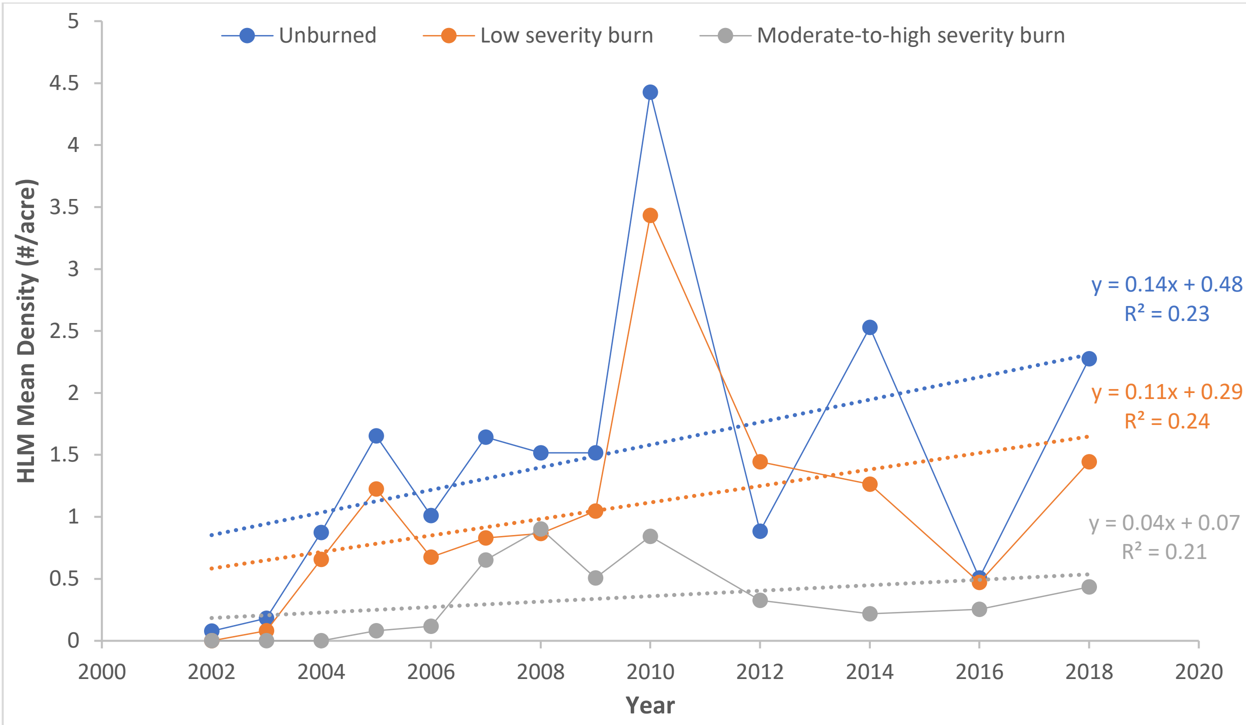

Figure 15. Mean density of Hlm over time per burn severity class after the Hayman Fire.

Dotted gayfeather flowering stem density was the only variable with a strong ability to explain variability in Hlm density with a positive association to Hlm population size. The other three variables with explanatory power (distance to unburned habitat, dead trees, and annual temperature) were negatively associated with Hlm density (**Table 9**).

Table 9. Unconditional parameter estimate (β_i), unconditional standard error, and 95% confidence intervals for the top 10 supported Hlm habitat models.

			95% Confidence Interval	
Variable	**βi**	**SE**	**Lower**	**Upper**
Density of Liatris punctata	0.0011	0.0005	**0.00**	**0.0022**
Growing season precipitation	0.05	0.04	-0.03	0.12
Distance to unburned skipper habitat	-0.0005	0.0001	**-0.0008**	**-0.0002**
Density of dead trees	-0.008	0.003	**-0.02**	**-0.003**
Annual temperature	-0.15	0.07	**-0.3**	**-0.009**
Growing season temperature	0.05	0.05	-0.19	0.16
Burn intensity experienced by sampled plots	-0.19	0.14	-0.46	0.08
Relative frequency of blue grama	0.004	0.004	-0.004	0.01
Density of live trees	0.003	0.002	-0.0009	0.01
Annual precipitation	-0.05	0.04	-0.13	0.03

[1] Values of the 95% confidence intervals for the unconditional parameter estimate (β_i) that do not overlap zero are shown in bold font.

Discussion – Hlm Population and Habitat Response to Wildfire

As described previously, skipper densities were the lowest ever recorded during the 2002 adult flight season, believed to be the consequence of a severe winter and spring drought. Hlm was nearly absent from unburned transects in 2003, and then began to recover to numbers greater than one skipper per acre from 2005 through 2021 (exceptions were 2012 and 2016). This recovery pattern parallels the density recovery observations made at the Trumbull forest thinning transects (Upper South Platte Watershed Restoration Project Surveys).

Hlm densities on low and moderate-to-severely burned transects were consistently lower, but not statistically different from those in the unburned areas over the entire sampling period (**Table 8** and **Figure 15**). However, regression of skipper density against dead tree density and distance from unburned forest was significantly negative, indicating that habitat recolonization occurred at lower rates in burned areas. Hlm habitat preferences may have been altered by the number of standing dead trees that allowed greater insolation in the understory. Hlm density regression against annual temperature was also significantly negative, suggesting that a more open understory after burning may have resulted in increased evaporation from exposed soils, and greater soil moisture stress on the larval foodplant. This negative relationship between skipper density and annual temperature is the same as that observed for the Trumbull thinned tree transects but may be amplified by the large number of burned dead trees that no longer contribute overstory canopy shade.

Density of flowering stems of dotted gayfeather increased significantly on the low severity and moderate-to-high severity burn transects (**Figure 16**). This result is attributed to the release of understory species from competition with trees for soil moisture and light. The significant Hlm density increase in relation to increased gayfeather stem density is likely a result of better opportunities to observe skippers when large numbers of nectar plants are available. Gayfeather density does not appear to be a key factor in predicting skipper density on its own; abundant gayfeather flowering stems represent a positive response to higher precipitation. As noted for the Upper South Platte Restoration study, gayfeather flowering stem densities on the Trumbull control transects are lower relative to transects on the thinned treatments, but skipper densities have been consistently higher over time.

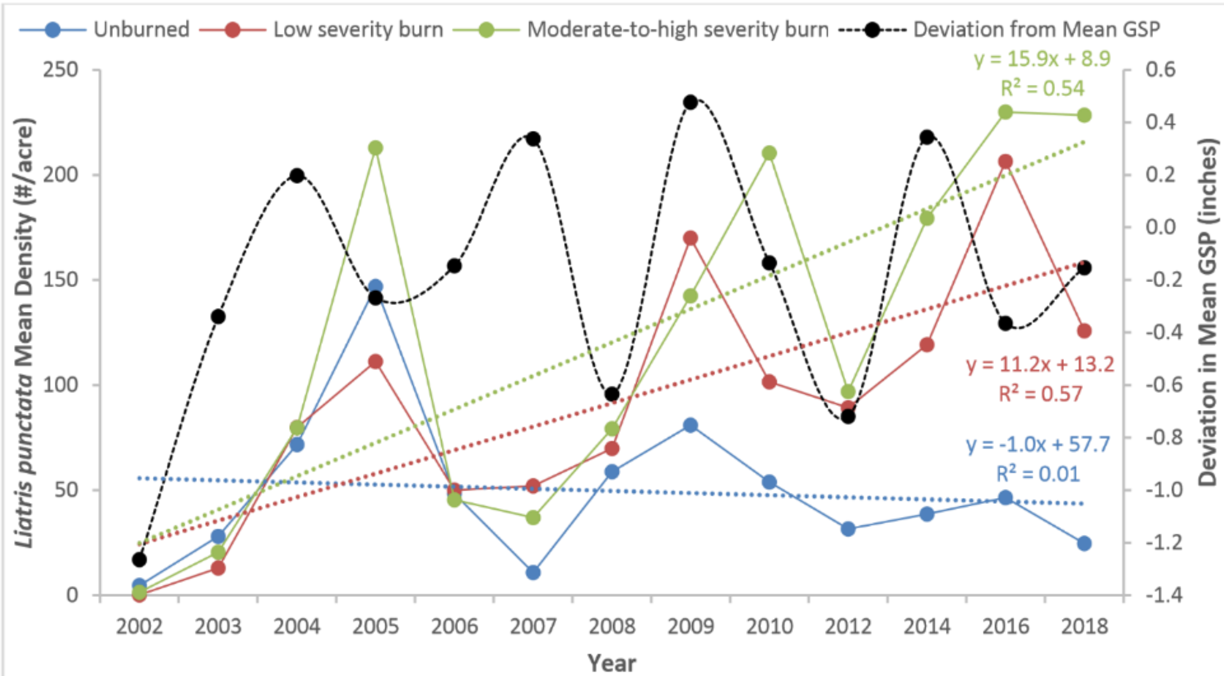

Figure 16. Dotted gayfeather flowering stems per acre by burn class for all years monitored (along with their linear trend lines). The mean deviation from growing season precipitation for each of the 19 years is also shown. Mean growing season precipitation is calculated from the period 1985-2009 using data from the Cheesman Reservoir weather station.

Supplemental Investigations

Field Surveys

The following are summaries of four supplemental Hlm field surveys conducted within the Upper South Platte Watershed study area for the purposes of monitoring skipper densities in areas burned by the 1996 Buffalo Creek and 2000 Hi Meadow fires, estimating skipper density in additional areas of fuel reduction and forest restoration treatments, and documenting a survey conducted near the outer boundary of mapped suitable habitat. Locations of these surveys are identified on **Figures 17 and 18**.

<u>Post-Buffalo Creek Fire Hlm Monitoring</u>. The USDA Forest Service and CNHP established five transects to monitor Hlm responses after the 1996 Buffalo Creek Fire in Jefferson County (Figure 17). Buffalo Creek was sampled from 2003 through 2005 and again in 2017. Hco have persisted at the Buffalo Creek transects since the fire at that location in 1996. However, no Hlm were recorded at Buffalo Creek in 2017 and future monitoring would be required to determine if Hlm still persists at the Buffalo Creek transects. The general trend was a statistically insignificant decline in Hlm numbers between initiation of sampling in 2003 and the last sample year of 2017 (linear regression on Hlm density/acre, $p = 0.54$). In contrast, pooled numbers of *Hesperia* skippers (Hlm plus Hco) showed an insignificant increase at the Buffalo Creek site over the period sampled (linear regression on *Hesperia* skippers/acre, $p = 0.65$. The average population density over the four years sampled was 0.8 Hlm/acre (range 0.7 to 1.3) and 1.5/acre (range 1.0 to 2.2) for *Hesperia* skippers. Results of a one-way ANOVA on skipper density by year show that the differences in skipper densities for Hlm ($p = 0.48$) and *Hesperia* skippers ($p = 0.22$) were not statistically significant ($p=0.48$) among the years sampled (one-way ANOVA on density/acre by year.

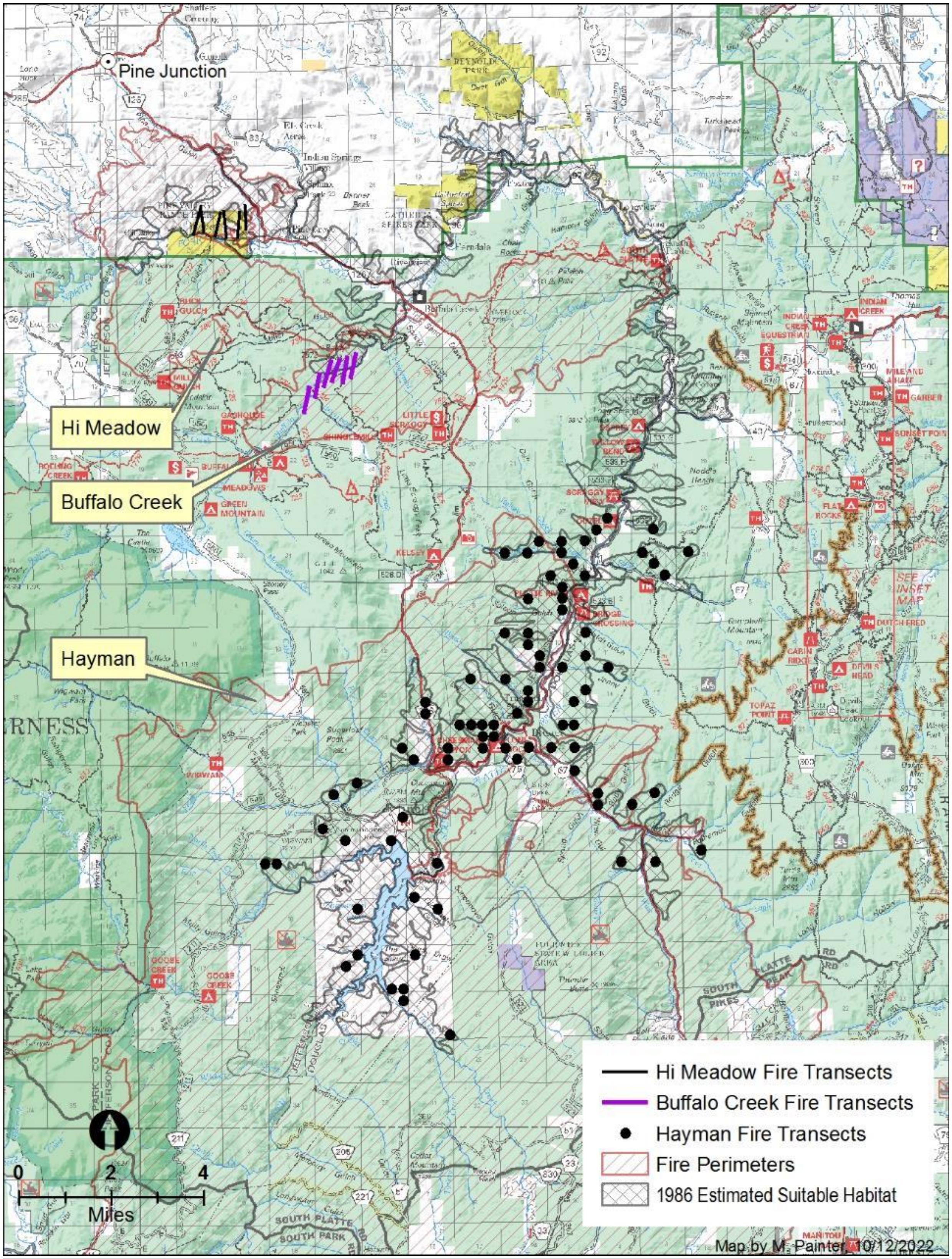

Figure 17. Survey locations for Pawnee montane skippers in the burn areas of the Hayman fire (83 initial sites, of which 32 were repeated), the Buffalo Creek fire (6 transects), and Hi Meadow fire (6 transects).

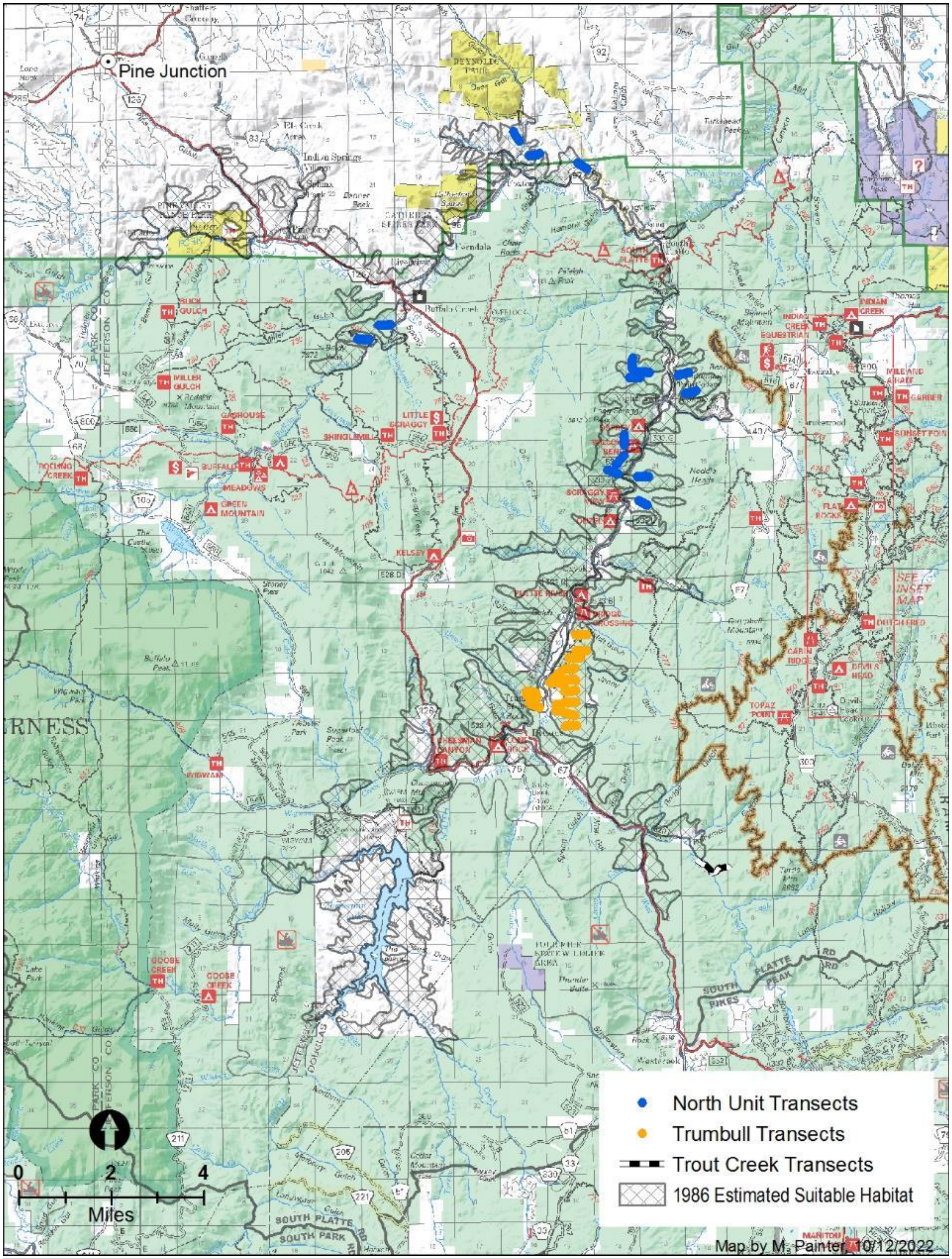

Figure 18. Survey locations for Pawnee montane skippers in areas of forest management activities: Trumbull, North Unit, and Trout Creek.

Post-Hi Meadow Fire Hlm Monitoring at Pine Valley Ranch Open Space Park. Jefferson County Open Space (JCOS) continues to monitor Hlm population responses to the Hi Meadow Fire that burned through Pine Valley Ranch Open Space Park in 2000. The park is located at the extreme northwestern edge of Hlm's range. The Hi Meadow burn area was sampled by CNHP from 2003 through 2005 and again from 2013 to 2021 except for in 2016 and 2020 by JCOS. The locations of the Hi Meadow transects are shown in **Figure 17**. Hlm were observed in all but two of the 10 years surveyed and Hco was observed in all 10 of those sample years. The average population density over those 10 years was 0.5 Hlm/acre (range 0 to 1.5) and 1.2/acre (range 0.1 to 4.4) for *Hesperia* skippers (Hlm plus Hco). Linear regression on skippers per acre at the Hi Meadow site over the period of monitoring shows a statistically insignificant decrease in numbers of both Hlm ($p = 1.3$) and *Hesperia* skippers ($p = 0.84$).

North Unit Vegetation Treatments and Hlm Responses. The South Platte Restoration monitoring initially (2000 - 2016) focused on forest treatments and Hlm in a localized area around Trumbull in the central part of their range. This localized monitoring did not capture treatments and Hlm responses in the northern half of their range, potentially missing trends that may differ from the relatively small area around Trumbull. In 2017, the USDA Forest Service and CNHP created 15 new transects to monitor Hlm densities in the northern part of their range (Sovell 2020b, 2022b) (**Figure 17**). These "North Unit" sites are similar in forest thinning treatments to the Trumbull sample sites and will each be sampled once in odd years. To date, these sites were visited in 2017, 2019 and 2021. Over this monitoring period, there was an average of 1.7 Hlm per acre at the North Unit sites (range 0.9 to 4.2), compared to an average of 6.2 Hlm per acre at the Trumbull Control site over the same three sampling years (range 3.1 to 12.0). When analyzed individually by site, the values for density were not statistically different among the new North Unit sites or between those sites and the Trumbull Control area, indicating that *Hesperia,* including Hlm, in the North Unit occur in numbers like or slightly below those of the Trumbull Control. Three samples in 6 years are not adequate to assess trends in Hlm density and statistically there has been no discernible pattern in Hlm density over this period. Host plant conditions were similar among the North Unit transects. This limited skipper sampling indicates ongoing forest restoration and fuel reduction treatment conditions are compatible with the persistence of Hlm in the northern portion of its distribution.

Trout Creek Hlm Survey. In 2010, a non-profit group, Wild Connections, contracted CNHP to survey Hlm along two trail corridors adjacent to Trout Creek in the Pike National Forest in Douglas County (Sovell 2010a). The study site is located in the extreme southeastern part of the skipper's range where little other monitoring has occurred (**Figure 18**). The objectives of the study were to: 1) understand how reclamation of a section of the trail corridor running east from the creek up a steep gully improves habitat for Hlm, 2) determine if Hlm inhabits the trail corridor on either of the two surveyed transects, and 3) identify suitable habitat at the survey site. The survey documented both suitable habitat for Hlm and the skippers themselves on the two transects. Documentation of a female Hlm attempting to oviposit suggests that Hlm is successfully reproducing at the survey site.

Hesperia Genetic Investigations

In 2015, 2016 and 2018, the USDA Forest Service conducted genetic analyses of *Hesperia* specimens collected across the range of Hlm and beyond (USDA Forest Service 2016, 2017, 2018, 2020). Samples were taken from museum specimens and from contemporary specimens collected for the study. The contemporary specimens included 5 individuals collected along the main stem of the South Platte River 4 miles south of Cheesman Reservoir and the 1986 study area (**Figure 19**). The intent was to investigate genetic diversity within the Hlm subspecies range and compare Hlm genetics to other *Hesperia* congeners. The methods and results are detailed in USDA Forest Service reports from the National Genomics Center for Wildlife and Fish Conservation (see USDA Forest Service 2016, 2017, 2018, 2020). Samples were analyzed first by using the cytochrome c oxidase subunit I (COI) region of the mitochondrial genome to determine species and haplotypes. Additional samples from specimens in the C.P. Gillette Museum of Arthropod Diversity collection were also analyzed to determine haplotype relationships across the greater North American range of *Hesperia leonardus* and its various subspecies. In total, 199 out of 255 contemporary and museum specimens analyzed were classified as part of the *H. leonardus* haplotype network. The contemporary Hlm samples (n = 63) were further analyzed for single nucleotide polymorphism (SNP) genotyping to determine current population structure within the range of Hlm.

All *H. leonardus* haplotypes were highly distinct (i.e., separated by a difference of multiple DNA base-pairs) from other *Hesperia* species haplotypes (e.g., those for Hco). In total, 8 unique *H. leonardus* haplotypes were observed, including one common haplotype that was represented in almost every sampling location across North America (USDA Forest Service 2016, 2017, 2018). Three haplotypes characterized the Hlm samples and 2 of those were not found in other *H. leonardus* samples. It was not possible to distinguish *H. leonardus* subspecies from one another based on the observed COI haplotypes.

Population structure analysis of contemporary Hlm samples using SNP genotyping revealed gene flow throughout the range of Hlm, but clusters of more related individuals were distinguishable along a geographic gradient (USDA Forest Service 2020). Individuals in the northern part of the range along the North Fork of the South Platte River shared more similarity with each other than they did with individuals from the main stem of the South Platte River and vice versa (**Figure 20)**. Two individuals, male Hlm 400 and female Hlm 401, collected 4 miles south of the 1986 study area were noticeably different in the SNP analysis. Although their COI results identified them as *H. leonardus* (USDA Forest Service 2017) and they are considered to be Hlm, their SNP markers were placed in a cluster separate from the other specimens. The location of these two specimens indicates that Hlm suitable habitat should be remapped to include more terrain south of Cheesman Reservoir. The area includes remnants of ponderosa pine forest with blue grama and dotted gayfeather that survived the Hayman Fire. Further investigations should be conducted to determine if this cluster represents a component of genetic diversity that was present before the fire and whether individuals at this site are now genetically isolated.

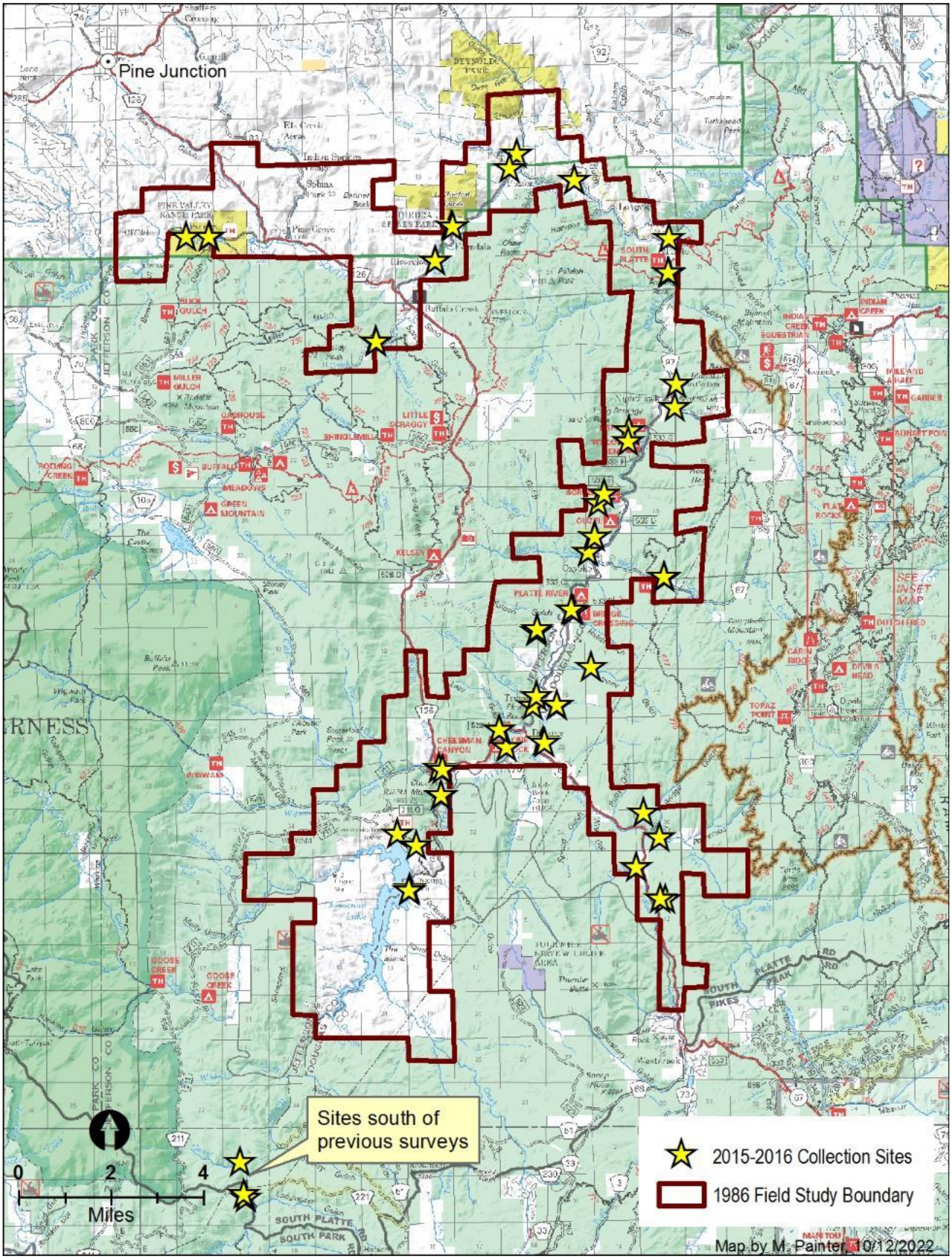

Figure 19. Sites where *Hesperia* butterflies were collected in 2015 and 2016 for genetic analysis.

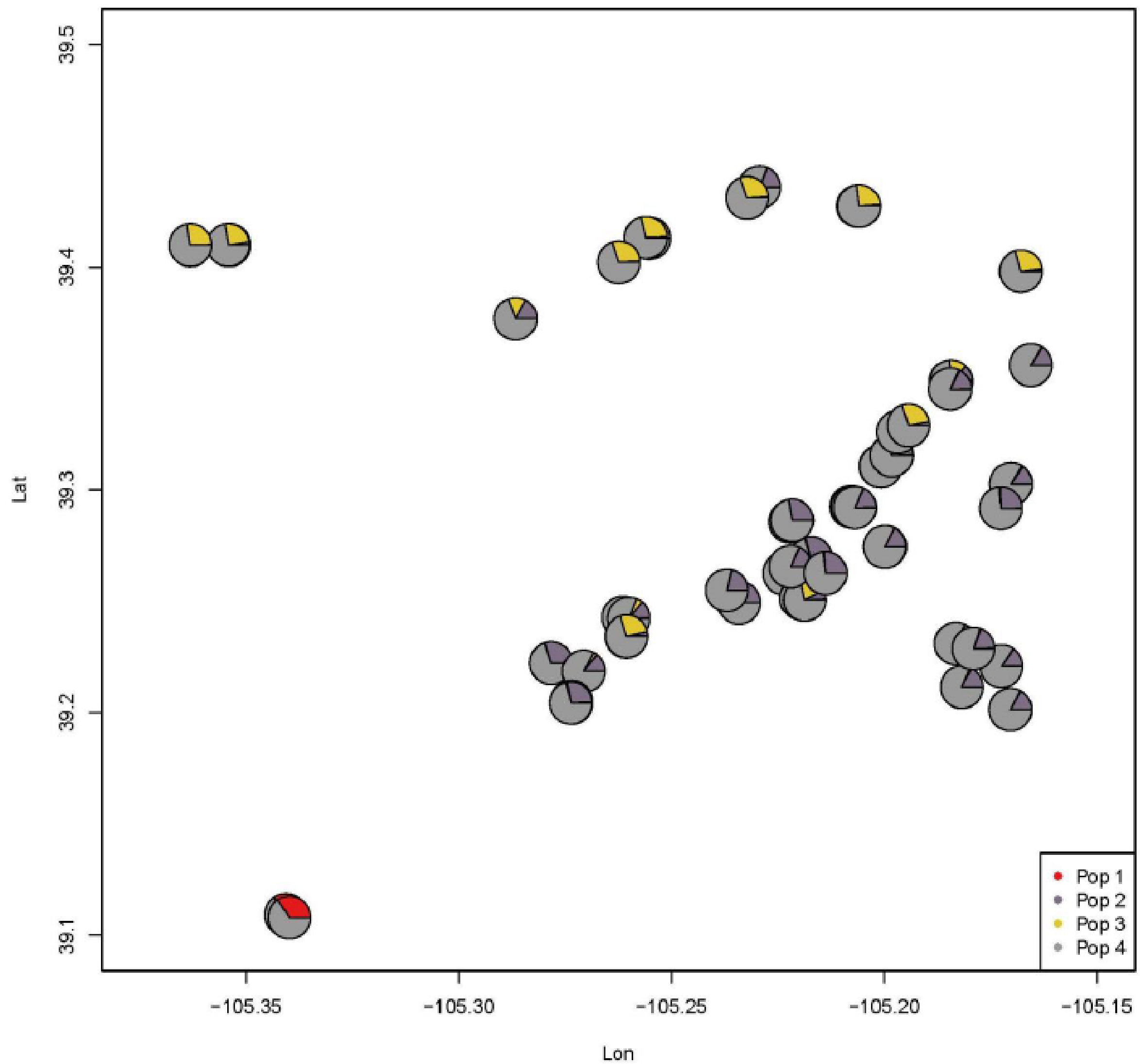

Figure 20. *Hesperia leonardus* montana: pie chart showing individual membership proportions to each SNP population cluster; individuals are graphed by latitude and longitude. Samples HLM 400 and HLM 401 are in the lower left.

Summary and Conclusions

The 1986 Two Forks Reservoir field surveys demonstrated that Hlm fully occupies its suitable habitat at low adult densities (generally 4 skippers or less per acre). The habitat for Hlm is defined by ponderosa pine woodlands of low canopy cover (30 percent), low density of mature conifers (≤40 trees per acre with dbh of 9 inches or greater); sparse conifer saplings and other shrubs in the understory; and blue grama and dotted gayfeather almost always present in the understory. The Hlm habitat suitability map shows that Hlm has historically occupied a relatively continuous habitat within the North Fork and main stem of the South Platte River with no major non-habitat gaps.

The 1986 field measurements provided an average abundance estimate for Hlm that ranged from 77,000 adult skippers (distribution survey sampled between August 14 and 28) to 141,000 individuals (census survey sampled between August 21 and 27) within the overall suitable habitat. If the Two Forks Reservoir were built, approximately 21 percent of the Hlm suitable habitat would be inundated, and from 20 to 40 percent of the skipper population would be lost, inferred from the 1986 skipper density measurements.

The overall pattern of skipper densities at the Trumbull forest thinning transects is interpreted as recovery from the 2001-2002 drought through 2007, then density variability from year to year in response to below average precipitation and higher than average temperatures (2008, 2011-2012, 2016-2017), but a general trend of increasing population size through 2021. Long-term monitoring at the Trumbull forest treatment sites shows that Hlm has maintained and increased its population over this twenty-year period within the weather regime that has occurred. From the adult skipper density patterns observed in this study, and the weather record at Cheesman Reservoir, an important risk to the Hlm population stability appears to be short-term winter and spring droughts that may negatively affect survival of post-diapausal larvae. A long-term increase in annual temperature represents an overall increased stress risk to the plant community and associated herbivores. These stress factors include higher evapotranspiration rates resulting in longer periods of low soil moisture and delays and suppression of plant growth and flowering during the growing season.

The forest thinning treatments that were implemented at Trumbull from 2000 through 2004 are compatible with the continued survival of Hlm. These thinning treatments contributed to the persistence, and some expansion in the cover and density of blue grama grass and dotted gayfeather, both of which are key Hlm habitat elements. A tree thinning pattern that preserves a relatively homogenous conifer cover of approximately 30 percent, and 100 trees (5 inches or greater in diameter) per acre appears optimum for maintenance of Hlm habitat. Small interspaces (0.1 acre or less) within the woodland provide important spatial components for adult skipper mate location, female oviposition, and nectaring. Hlm avoids larger open patches (1 acre or greater) within the woodland, based on observations made both in treatment clear cuts and in naturally occurring patches in undisturbed habitat. This long-term monitoring study confirms that Hlm is primarily a woodland species, in contrast to the nearby populations of the Pawnee skipper (*H. leonardus pawnee*), which is an open grassland species.

Post-Hayman fire skipper monitoring in moderately to intensively burned areas indicates a slow skipper population recovery over time. The understory plant community, including blue grama and dotted gayfeather, is highly resilient to fire and recovers immediately. Overstory ponderosa pine and Douglas-fir trees killed by fire will likely require 50 to 100 years or more to regain equivalent canopy cover. Skipper monitoring indicates that Hlm occurrence is negatively associated with standing dead trees, which may mean that intensely burned areas will remain sparsely inhabited over the long term. This avoidance behavior by Hlm adults means that crown fires that kill all or most mature conifers represent a significant risk to the suitable habitat extent for this species.

With the advent of fire suppression in the early 1900s, there has been a trend toward greater forest canopy closure and increased dominance by Douglas-fir. This trend indicates a long-term overall reduction in Hlm habitat, assuming the continued practice of fire suppression. This trend is being offset by implementation of forest thinning treatments that have resulted in more open woodland habitats favorable for use by Hlm. However, the Hayman Fire of 2002 demonstrated that very large wildfires can burn a large fraction of the Hlm habitat in one event, thus reducing or eliminating Hlm use of burned woodlands for long periods of time.

Supplemental field surveys show that Hlm may have persisted to the present in areas burned by the Buffalo Creek Fire in 1996 and has persisted within the 2000 Hi Meadow Fire area in the northern portion of the skipper range. Range extensions for Hlm were documented further upstream on the South Platte River mainstem south of Cheesman Reservoir, and on Trout Creek southeast of Deckers.

Analysis of the COI region of the mitochondrial genome showed *H. leonardus* haplotypes are distinct from other *Hesperia* species, but it was not possible to distinguish *H. leonardus* subspecies from one another based on the 8 observed COI haplotypes. One haplotype was found in nearly every North American sampling region, 2 haplotypes were only found in the Hlm sampling region, and 5 haplotypes were not found in the Hlm sampling region.

A subset of Hlm samples was further analyzed using SNP genotyping to determine population structure within the range of Hlm. The results indicate gene flow throughout the overall population, with some differentiation between samples from the northern part of the range and those from the southern. The SNP markers for two individuals sampled from the mainstem South Platte southwest of Cheesman Reservoir were placed in a cluster separate from the other specimens. This southern collection site includes remnants of ponderosa pine forest with blue grama and dotted gayfeather that survived the Hayman Fire. More investigation is needed to determine if this finding indicates an isolated subpopulation.

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Leslie Ellwood of the USFWS participated in the Hlm listing process and preparation of the Recovery Plan and was actively involved in the early years of skipper monitoring at Trumbull. She continues to support monitoring and recovery efforts as lead biologist for Hlm at the USFWS Colorado Field Office.

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